



Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal

KHEM RAJ BHATTARAI* and OLE R. VETAAS†

*Department of Botany, University of Bergen, Allégaten 41, N-5007 Bergen, Norway, E-mail: Khem.Bhattarai@bot.uib.no and †Centre for Development Studies, University of Bergen, Nygaardsgaten 5, N-5015 Bergen, Norway

ABSTRACT

Aim To explore the variation in species richness along a subtropical elevation gradient, and evaluate how climatic variables explain the richness of the different life forms such as trees, shrubs, climbers, herbs and ferns.

Location The study was made in a subtropical to warm temperate region in the south-eastern part of Nepal, between 100 and 1500 m above sea level (a.s.l.).

Methods The number of species was counted in six plots (50 × 20 m) in each of the 15 100 m elevation bands covering the main physiognomic structures along an imaginary transect. Each species recorded was assigned to a life form. Potential evapotranspiration (PET, i.e. energy), mean annual rainfall (MAR), and their ratio (MI = moisture index) were evaluated as explanatory variables by means of generalized linear models (GLM). Each variable was tested individually, and in addition MAR and PET were used to test the water-energy dynamics model for each life form.

Results The richness of herbaceous species, including herbaceous climbers, was unrelated to any of the climate

variables. PET was strongly negatively correlated with elevation, and the following relationships were found between increasing PET and richness: (i) shrubs, trees and total species (sum of all life forms) showed unimodal responses (ii) ferns decreased monotonically, and (iii) woody climbers increased monotonically. Richness of all woody groups increased monotonically with MAR and MI. The water-energy dynamics model explained 63% of the variation in shrubs, 67% for trees and 70% for woody species combined.

Main conclusions For the various herbaceous life forms (forbs, grasses, and herbaceous climbers) we found no significant statistical trends, whereas for woody life forms (trees, shrubs, and woody climbers) significant relationships were found with climate. E.M. O'Brien's macro-scale model based on water-energy dynamics was found to explain woody species richness at a finer scale along this elevational-climatic gradient.

Key words climatic variables, elevation gradient, macroecology, Nepal, species richness, subtropics, water-energy dynamics, woody plants.

INTRODUCTION

Variation in species richness with elevation has been known for over a century (Wallace, 1878; Pianka, 1966; Brown & Davidson, 1977; Lomolino, 2001). Several studies have found a decreasing trend in species richness with increasing elevation (e.g. Yoda, 1967; Alexander & Hilliard, 1969; Kikkawa & Williams, 1971; Hamilton, 1975; Wolda, 1987; Gentry, 1988; Navarro, 1992; Stevens, 1992; Patterson *et al.*,

1998), whereas others have found a hump shaped relationship between species richness and elevation (e.g. Janzen, 1973; Whittaker & Niering, 1975; Rahbek, 1995; Lieberman *et al.*, 1996; Gutiérrez, 1997; Fleishman *et al.*, 1998; Odland & Birks, 1999; Grytnes & Vetaas, 2002). The mechanistic reasons for these patterns are a matter of on-going debate (see Rohde, 1992; Rahbek, 1995; Rosenzweig & Sandlin, 1997; Rosenzweig, 1997; Brown, 2001; Lomolino, 2001; Whittaker *et al.*, 2001), and it is not yet known whether a universal explanation exists (Colwell & Hurtt, 1994; Rahbek, 1995, 1997).

The elevation gradient of species richness is intricately related to species-latitude and species-area relationships

* Corresponding author.

(Lomolino, 2001). Körner (1999) argues that elevation gradients can contribute important insights into developing a general theory of species diversity. The elevation gradient in the species richness pattern is commonly explained by similar factors to the latitudinal gradient, such as climatic factors, productivity, and other energy-related factors (Richerson & Lum, 1980; Turner *et al.*, 1987; Currie, 1991; Rohde, 1992; Wright *et al.*, 1993; Grytnes *et al.*, 1999). Lomolino (2001) pointed out that many components of climate and local environment (e.g. temperature, precipitation, seasonality and disturbance regime) vary along the elevation gradients and ultimately create the variation in species richness. Species richness studies from temperate zones stress the importance of energy as a limiting factor (e.g. Currie, 1991), whereas tropical studies emphasize the importance of moisture and related factors (e.g. Gentry, 1982; Brown, 1988). The macro-scale study of O'Brien (1993, 1998) and O'Brien *et al.* (1998) from Southern Africa, found that geographical gradients in plant species richness are the by-product of water-energy dynamics. O'Brien (1993, 1998) proposed a model that species richness is a linear function of water plus a parabolic function of energy [species richness = water + energy-(energy)²], and claimed that this model can be applied to explain the woody species richness pattern everywhere on the earth. This model, so far as we know, has not been tested on an elevation gradient. Thus, one of the main aims of our study was to evaluate the explanatory power of this model on species richness patterns along an elevation gradient.

Factors causing variation in species richness may differ between different organisms and between life forms of plants. Huston (1994) found that trees and herbaceous species have different responses in eastern compared to central and North America. A comparison of various life forms may allow a finer resolution of precise causal factors than studies on total plant richness. Thus, in the present study, we analysed the richness of different life forms along a subtropical elevation gradient (100–1500 m a.s.l.) in eastern Nepal.

The general pattern in total plant species richness in each 100 m elevation zone (i.e. gamma diversity, *sensu* Lomolino, 2001) has been estimated by Grytnes & Vetaas (2002). They used interpolation of presences between the extreme recorded altitudinal ranges based on published data, and found a monotonic increasing trend in total species richness from 100 to 1500 m a.s.l. However, they also demonstrated that the interpolation method combined with low sampling intensities may under-estimate species number at the gradient extremes (Grytnes & Vetaas, 2002; Vetaas & Grytnes, 2002). Thus, a lower species richness in the subtropical lowland compared to the elevated warm temperate zones may be an artefact. Lomolino (2001) argues that sampling biases or low sampling intensity seriously affect the species richness pattern along the elevation gradient (see also Terborgh, 1977; Wolda, 1987; McCoy, 1990; Colwell & Hurtt, 1994; Rahbek, 1997). Rahbek

(1995) made a compilation of literature and found that only 21% of studies are based on standardized survey effort, which makes it difficult to assess whether the variation in the pattern is real or due to an artefact of sampling. Therefore, we aimed to analyse species richness by using a fixed area and a standardized sampling effort. This study will ask the following major questions: (1) how does the species richness of different life forms (herbs, shrubs, trees, climbers and ferns) vary along the subtropical elevation gradient? (2) how well do the climatic factors explain the species richness of the different life forms? and (3) how does the water-energy-dynamics model (O'Brien, 1993, 1998) explain variation in the species richness pattern along the elevation gradient?

MATERIALS AND METHODS

Study area

The study area is located in Sunsuri district, south-eastern Nepal. We used a transect from Simarban, Ithari, in the south (26°42'-N; 87°16'-E), to Telpuranda in the north (26°59'-N; 87°21'-E) (Fig. 1a).

Geomorphologically, the study transect is situated in the northern part of the Indo-Gangetic plain (which is called Terai) and part of the Mahabharat range (Lesser Himalaya) (Fig. 1b). Terai is an east–west orientated lowland plain (c. 30–40 km wide) with an average elevation of 100–300 m above sea level (a.s.l.). The Siwalik is a sub-Himalayan range (c. 1300 m a.s.l.), and is the youngest in the formation of the mountain system (Manandhar, 1999), but in the study area (i.e. east Nepal) the Siwalik is merged with the Mahabharat range (Pandey, 1995). This Mahabharat zone consists of highly deformed and recrystallized sedimentary and igneous rocks (Hagen, 1969).

The climate of Nepal falls within the monsoon system of the Indian subcontinent, with dry periods in winter and wet periods in summer. Pronounced rainfall occurs during the months of June to September. There is a hot monsoon climate with hot, wet summers and mild warm dry winters up

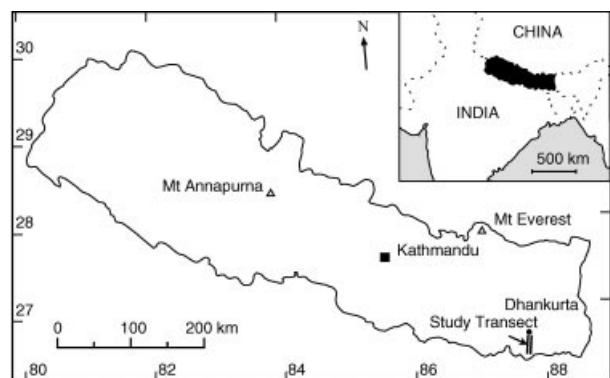


Fig. 1a Location of the study area in south-east Nepal.

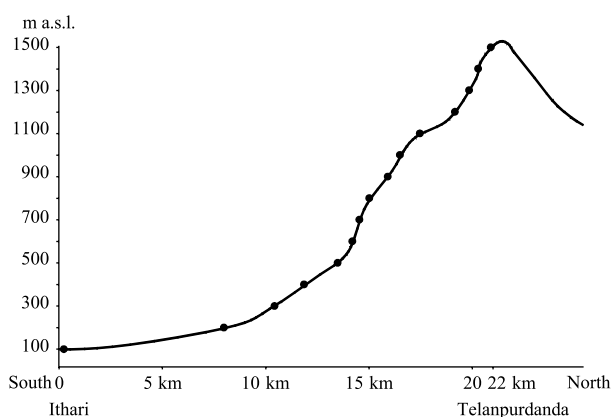


Fig. 1b Schematic cross-section of the investigated elevation transect from Ithari (100 m a.s.l.) to Telpurpurdanda (1500 m a.s.l.). Black dots indicate the location of the sampled elevation bands.

Table 1 Plant species richness, Mean annual temperature (MAT), potential evapotranspiration (PET), mean annual rainfall (MAR), and moisture index (MI) along the studied elevation gradient in eastern Nepal

Elevation m a.s.l.	Total number of species	MAT (°C)	PET (mm)	MAR (mm)	MI
100	212	24.70	1455.57	2001.33	1.37
200	241	24.45	1440.84	2148.06	1.49
300	225	24.24	1428.46	2216.79	1.55
400	262	24.03	1416.09	2254.05	1.59
500	234	23.59	1390.16	2261.91	1.63
600	267	22.80	1343.60	2201.82	1.64
700	255	22.20	1308.25	2072.67	1.58
800	256	21.54	1269.35	1902.18	1.50
900	208	20.94	1233.99	1718.41	1.39
1000	229	20.21	1190.98	1549.43	1.30
1100	222	19.70	1160.92	1423.30	1.23
1200	241	19.09	1124.97	1368.26	1.22
1300	237	18.48	1089.03	1408.31	1.29
1400	207	17.86	1052.49	1476.56	1.40
1500	207	17.24	1015.95	1495.14	1.47

to 1000 m a.s.l., but in the Mahabharat range between 1000 and 2000 m a.s.l. there is a warm temperate monsoon climate with warm and wet summers and cool and dry winters. Mean annual temperature at 100 m a.s.l. is 24.7 °C and declines by 0.53 °C per 100 m elevation (adiabatic lapse rate in the studied transect), and the mean annual precipitation is 2001 mm (Table 1). Cloud formation starts above *c.* 1400 m a.s.l. and occurs frequently at *c.* 2000 m a.s.l. in the lesser Himalayas, whereas cloud formation is normally between 2500 and 3200 m a.s.l. in the greater Himalayas (Dobremez, 1976).

Nepal lies in the subtropical zone, i.e. just north of latitude 23°N. The vegetation of Nepal has been described by several

phytogeographers (e.g. Banerji, 1963; Hara, 1966; Stanton, 1972; Dobremez, 1976), and the elevation zone between 100 and 1000 m a.s.l. is commonly described as subtropical or tropical. The forests are dominated by the tropical species *Shorea robusta* (Dipterocarpaceae), and subtropical elements associated with the forests are *Adina cordifolia*, *Careya arborea*, *Dillenia pentagyna*, *Terminalia bellirica*, *Terminalia chebula*, *Lagerstroemia parviflora* and *Dalbergia sissoo*. Frost starts to occur from 1200 m a.s.l. and lower elevation species start to disappear. Between 1000 and 2000 m a.s.l. the warm temperate zone prevails and is dominated by *Schima wallichii* and *Castanopsis indica* forest. Other principal associated species are *Alnus nepalensis*, *Juglans regia*, *Michelia champaca*, *Toona ciliata*, *Ilex excelsa* and *Saurauia napaulensis*. The region above 2000–3000 m a.s.l. falls into the cool temperate region and above 3000–4000 m a.s.l. is the subalpine region. The timberline is *c.* 3900–4100 m a.s.l. in the Nepal Himalayas (Mani, 1978).

The study transect passed through subtropical forest dominated by *Shorea robusta*. Most of the area below 200 m a.s.l. has been utilized for rice production, but there are still patches of forest left. The compression of subtropical and warm temperate life zones over a short distance (22 km) along the transect, makes it rich in biodiversity. Siwakoti & Verma (1999) reported a total of 743 species from this region but they collected from a much broader region and limited their collection to above 600 m a.s.l. The flat land of Terai is very intensively cultivated. There are also terraces on the hill slopes but they are less intensively cultivated.

Field sampling

The field sampling was carried out from 20 June – 15 July, 2001. An imaginary transect line was made in a north–south direction. The transect starts from Simarban, Ithari at 100 m a.s.l. in the south and ends at 1500 m a.s.l. in Telpurpurdanda in the north. Six plots (50 × 20 m) were made in each 100 m elevation band (Fig. 1b). The plot size of 0.1 ha has been used in several diversity studies (e.g. Whittaker, 1963, 1966; Whittaker & Woodwell, 1969; Whittaker & Niering, 1975), which facilitates biogeographical comparison of species richness (Clinebell *et al.*, 1995). Thus, floristic data were obtained from a total of 90 plots, 0.6 ha for each 100 m elevation band in 15 bands (total area = 9 ha).

The sampling followed certain criteria in order to cover the most common physiognomic types of vegetation in each 100 m elevation zone. All plots sampled were chosen because they were representative of the most common vegetation of a certain physiognomic type in each elevation band. We sampled two plots in open herb-dominated vegetation, two plots in shrub-dominated vegetation, and two plots in the most common types of forest. An exception to this is at 1500 m a.s.l., where we sampled four plots in forest and two plots in shrub-

dominated vegetation because of an abundance of forest and an absence of open land available for sampling. An altimeter (with an accuracy of ± 10 m) was used regularly to fix the altitudinal position along the transect line. The altimeter was calibrated each day before sampling with the help of a topographic map. Each plot was sampled exhaustively (2–4 h by 4 persons) and the plot area was kept constant thus controlling both sampling effort and area in our measure of species richness (Rahbek, 1997; Lomolino, 2001). All vascular plant species, including ferns and fern allies, were recorded and assigned to a life form, such as herbs, shrubs, trees, climbers and ferns. The herbaceous group was divided in two, i.e. grasses and nongrasses (forbs). The climbers were divided into woody and herbaceous climbers. Climbers, trees, and shrubs correspond to the main life form groups of Raunkiaer, such as lianas, phanerophytes (trees), nano phanerophytes and chamaephytes (shrubs). The herbaceous group is most heterogeneous and consists of several life forms defined by Raunkiaer. The division follows the rationale of other studies, which have studied an individual life form, e.g. ferns in Mexico (Tyron, 1989), Bolivia (Kessler, 2000) and Malaysia (Md. Nor, 2001), herbs in New Zealand (Ohlemüller & Wilson, 2000), trees and shrubs in southern Africa (O'Brien, 1993, 1998), and climbers in Mexico (Vazquez *et al.*, 1998). In addition, we subtracted ferns from the total number of species, i.e. to give flowering plant species, which is comparable with the results in Grytnes & Vetaas (2002).

Species not identified in the field were taken to the National Herbarium of Nepal (KATH) for identification. Nomenclature follows Hara *et al.* (1978); Hara & Williams (1979) and Hara *et al.* (1982) for flowering plants and Iwatsuki (1988) for ferns.

Climatic variables

The climatic variables used in this study are mean annual rainfall (MAR), potential evapotranspiration (PET) (i.e. energy) and a moisture index (MI). Mean annual temperature (MAT) and MAR were interpolated from the neighbouring stations because there are only three climate stations adjacent to the study transect. We used 17 different climate stations (records from 1971 to 1996) located along the transect (maximum distance is *c.* 35 km from the transect). The climate records are collected and published by the Department of Hydrology and Meteorology (DHM), Government of Nepal. We estimated a lapse rate of 0.53 °C/100 m elevation for mean annual temperature by linear regression ($r^2 = 0.98$; $P < 0.001$) (Fig. 2a). The temperature was interpolated between two-elevation bands based on a weighted average of the two closest climatic stations above and below each elevation band. Rainfall is not a simple linear function of elevation, and therefore we used a cubic smooth spline in Generalized Additive Model (GAM, Hastie & Tibshirani,

1990) with 4 degrees of freedom to estimate rainfall in each 100 m elevation band. We assigned a different weight to weather stations based on the distance between the transect and the location of the station, to account for the relative weight of that particular station on the interpolated rainfall.

The PET and MI were calculated based on the formula of Holdridge *et al.* (1971), [PET = mean annual Bio-temperature (i.e. temperature > 0 °C) $\times 58.93$; and similarly the MI = mean annual Bio-temperature $\times 58.93$ /mean annual precipitation]. For simplicity the moisture index was inverted, where a value below 1 indicates a negative water balance, and a value above 1 indicates a positive water balance (Vetaas, 2002). The PET is commonly used as a surrogate of energy (O'Brien, 1998), which is expressed in millimeters (mm) to measure the potential amount of water released through surface evaporation and transpiration from homogeneous covered vegetation (Currie, 1991). The greater the temperature, the greater the PET (Pianka, 1983).

Numerical analyses

The response variable, species richness in each 100 m elevation band, is defined as the total number of unique species present in the six 0.1-ha plots in each 100 m band. Thus it represents the density of species per 0.6 ha, but we use the term richness since it is not one big 0.6 ha plot but six plots of 0.1 ha. The climatic factors and elevation were used as explanatory variables. However, as both MAT and PET are almost perfectly negatively correlated with m a.s.l. ($r = -0.99$), only PET is used in the explanatory analyses.

A Generalized Linear Model (GLM; McCullagh & Nelder, 1989; Dobson, 1990) was used to relate species richness to the explanatory variables. The response variable, species richness, takes the form of discrete data (counts) and may have a Poisson distribution of error (McCullagh & Nelder, 1989), which requires a logarithmic link. The difference between a logarithmic link and an identity link function (assuming normal distributions of error) was assessed by drawing a diagnostic Q-Q-plot of the residual variation from preliminary tests (Crawley, 1993; Hastie & Pregibon, 1993). This indicated that the Poisson model had a slightly better fit, especially when the counts were low (e.g. for shrubs). When integers were high (e.g. total species > 200), the error distribution was almost indistinguishable from normal. Since we have a low degree of freedom (d.f. = 15) there is a high chance of over dispersion (cf. below); this was substantially reduced by using a logarithmic link, which also guaranteed that the fitted values were positive (Hastie & Pregibon, 1993). The first and second order polynomials of each variable were tested against no relationship and against each other. The two climatic variables, MAR and PET (energy) were used in a bi-variable model to check the explanatory power of the water-energy dynamics model (O'Brien, 1993, 1998). It should be noted

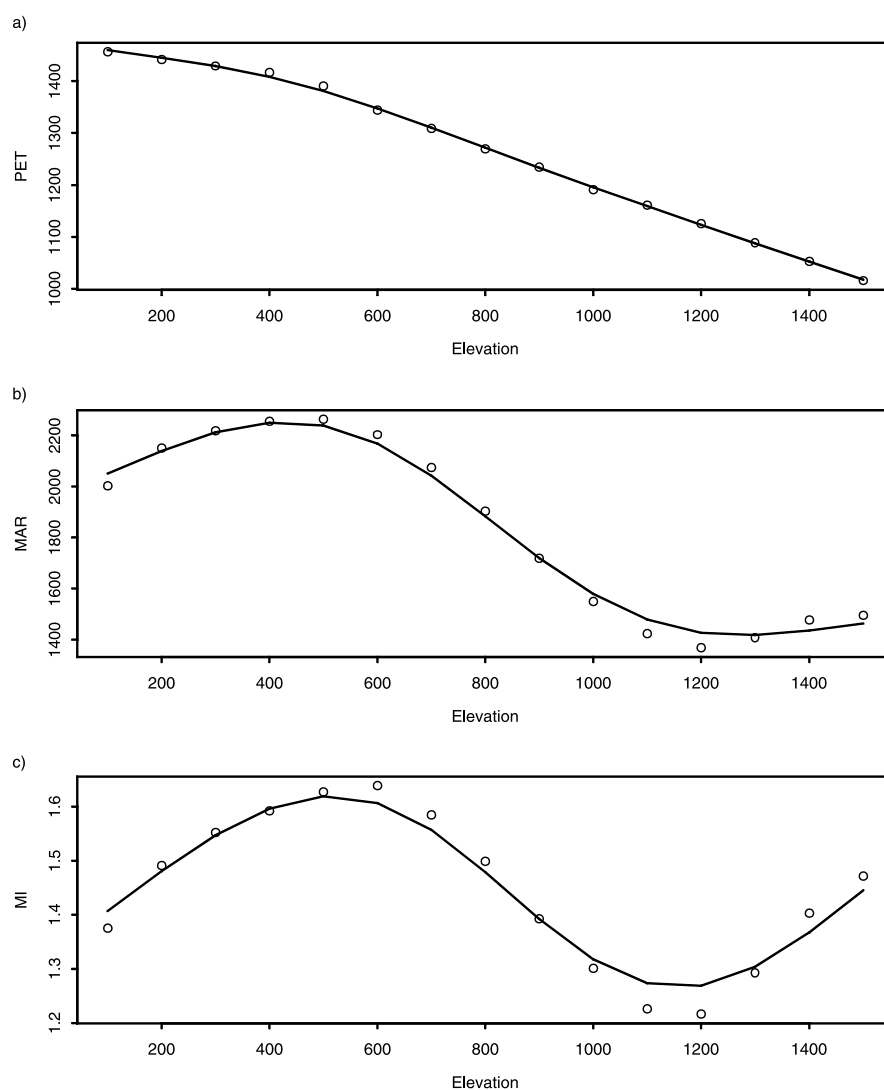


Fig. 2 Shows the relationships between elevation (m a.s.l. = x -axis) and (a) potential evapotranspiration (PET, mm); $r = -0.99$, (b) mean annual rainfall (MAR, mm), and (c) moisture Index (MI). General additive modelling with four degrees of freedom was used to fit the regression lines.

that O'Brien's empirical formulation is based on Thornthwaite's minimum monthly PET, as distinct from the formula used herein (above). The change in deviance between nested models of Poisson distribution was expected to be chi-square distributed. We used χ^2 tests, but in addition we used an F -test when severe over — or under — dispersion (dispersion parameter > 1.5 or < 0.5 , assumed to be 1), was detected in models of one variable (McCullagh & Nelder, 1989; Hastie & Pregibon, 1993).

Autocorrelation

The number of species in each 100-m interval is a variable that most probably exhibits distance decay (Tobler, 1969),

which means that species richness in two nearby elevation zones are on average more similar than species richness in distant zones (Vetaas & Grytnes, 2002). This type of positive autocorrelation is mainly a problem when explicit causal factors are being tested (Legendre, 1993; Lennon, 2000). Thus, when species richness is regressed against elevation (m a.s.l.) we did not take spatial autocorrelation into account. These results have primarily a descriptive value and do not follow the strict assumptions of inferential statistics because of spatial autocorrelation. Spatial autocorrelation describes the dependence between pairs of observations at given distances in space, and will reduce the degrees of freedom in statistical significance tests (Legendre, 1993). The raw-data consist of species richness in 90 plots (6×15 elevation bands), presum-

ably with autocorrelation occurring both within bands and between bands. From this data we extracted the number of unique species in each of the 15 bands (cf. above), and the degrees of freedom are reduced from 90 to 15. There is no autocorrelation within specific elevation bands, but between bands there may be autocorrelation. There are two fundamental different approaches to handle this: (1) statistically remove autocorrelated deviance before regression of environmental factors, and (2) check for autocorrelation in the residual variance after regression of environmental factors (Diniz-Filho *et al.*, 2003). We used the second approach since all the climate variables have a clear spatial structure (Fig. 2). The residual deviance was regressed against two spatial variables, i.e. the horizontal and vertical distance from the band below 100 m a.s.l., both in first and second order. We used S-plus (version 4.5) for regression analysis and graphical representation.

RESULTS

Species richness along the elevation gradient

We recorded a total of 966 species in this subtropical elevation transect. More than half of the species are herbaceous (53.7%), trees account for 17%, shrubs 12%, climbers 12%, and ferns 5.3% of the total species observed. The variation of total species richness along the elevation gradient is shown in Table 1. The lowest species richness is found at both ends of the gradient, 207 species at the top and 212 species below 100 m. Maximum species richness (267 species) is found at 600 m a.s.l., and above and below this elevation species richness gradually decreases (Table 1). There is also a hump-shaped pattern when the ferns were excluded from the total richness (i.e. for flowering plants) with maximum species richness between 600 and 800 m a.s.l. (Fig. 3, and Table 3).

The variation in richness for each life form along the elevation gradient is shown in Table 2. Except for climbers, the trends resemble those found for PET (Table 4, and Fig. 4I) since PET is almost perfectly negatively correlated with elevation ($r = -0.99$) (Fig. 2). The herbaceous species do not have significant trends in richness; this was also true for the herbaceous subgroups such as grasses and forbs (nongrasses). Only the woody climbers have a significant positive trend (Table 2), when climbers were analysed separately as two groups, i.e. herbaceous and woody climbers. The ferns have a positive monotonic increase with elevation. There is a hump-shaped pattern along the gradient for shrubs and trees separately, and for the woody species (shrubs + trees). These groups have maximum richness between 600 and 800 m a.s.l.

The same analyses, as above, were also done on species richness of the six plots in each elevation band ($n = 90$). This gave the same results as above with the exception of

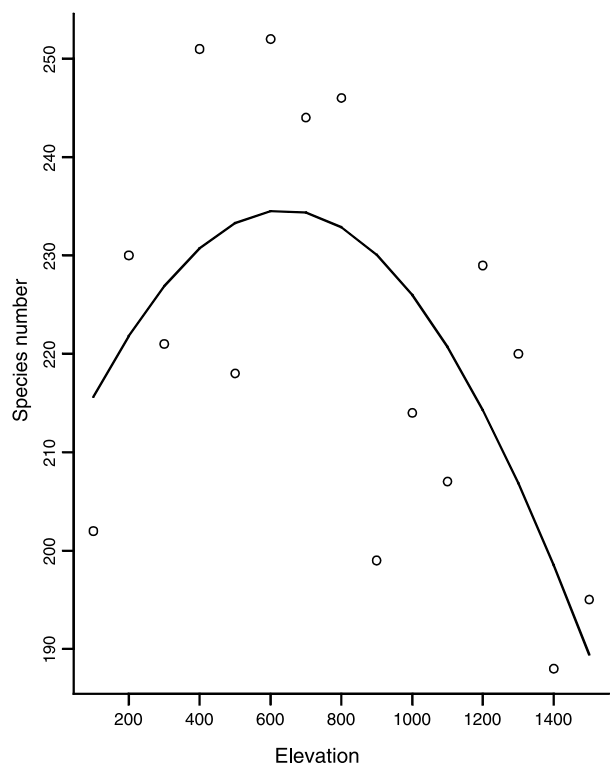


Fig. 3 The relationship between flowering plant richness (excluding ferns) and elevation (x -axis = m a.s.l.). The fitted line is based on a second order polynomial regression using a Generalized linear model. See Table 3 for regression details.

herbaceous species, which had a unimodal relationship with elevation, with a similar maximum.

Relationships between climate and species richness

The relationships between climate and richness for each life form are shown in Table 4 and Fig. 4. Total species richness has a hump-shaped or unimodal relationship with PET, indicated by a statistically significant second order term in the GLM analysis. Total richness also has a significant positive log linear relationship with the moisture variables MAR and MI, for the latter variable the second order term is also significant.

Shrubs are the only life form group that have regression models with high over-dispersion (i.e. 1.8–2), where the statistical significance depends on an F -test. There is a significant positive log linear relationship with MI, but the models for PET and MAR are not significant by the F -test but are significant according to a Chi-square test (Table 4). Trees have a significant unimodal response to PET, and a positive log linear relationship with the moisture variables MAR and MI. The residuals from each of these models (trees) have significant spatial structure, which indicates invalid or incomplete models.

Table 2 Summary of regression statistics when species richness of each life form is regressed against elevation. Polynomial first order (1) and second order (2) were tested against the null model and each other. The deviance explained indicates percentage of total (null) deviance

Lifeforms	Polynomial order	Degrees of freedom	Residual deviance	% deviance explained	P-value*
Total species	2	12	14.84	39.75	< 0.001
Shrubs	2	12	18.14	41.98	< 0.001
Trees	2	12	15.91	38.37	< 0.005
Climbers	1	13	14.43	19.49	ns
Herbaceous climbers	1	13	13.20	2.23	ns
Woody climbers	1	13	17.88	17.76	< 0.049
All Herbaceous	1	13	8.92	10.10	ns
Grasses	1	13	0.28	4.86	ns
Forbs	1	13	2.76	14.90	ns
Ferns	1	13	12.76	26.01	< 0.032

* using a χ^2 test.

Table 3 Summary of regression statistics when flowering plant species richness is regressed against elevation. Polynomial first order (1) and second order (2) models were tested against the null model and each other. The deviance explained indicates percentage of total (null) deviance. For graphical illustrations of the model see Fig. 4

	Polynomial order	Degrees of freedom	Residual deviance	% deviance explained	P-value*
Null deviance		14	27.25		
Flowering plants	1	13	22.39	17.83	< 0.027†
Flowering plants	2	12	14.92	45.21	< 0.006

† over-dispersion is high, and the *F*-test is not significant. * using a χ^2 test.

Table 4 Summary of regression statistics of each lifeform when related to climatic variables (PET, MAR, and MI). Only models with significant (Chi-test) polynomial first order (1) and/or second order (2) fits are shown. The deviance explained indicates the percentage of total (null) deviance. For graphical illustrations see Fig. 3

Lifeforms	Term	Ord	Degrees of freedom	%-deviance explained	P-value‡
Total species	PET	2	12	33.87	< 0.033
	MAR	1	13	24.17	< 0.014
	MI	1	13	21.01	< 0.021
	MI	2	12	46.53	< 0.012
Shrubs	PET	2	12	28.95	< 0.011*
	MAR	1	13	14.49	< 0.033*
	MI	1	13	28.17	< 0.002
Trees	PET	2	12	27.90	< 0.027†
	MAR	1	13	32.67	< 0.003†
	MI	1	13	45.93	< 0.001†
Climbers	PET	1	13	22.09	< 0.042
	MAR	1	13	32.75	< 0.015
	MI	1	13	28.85	< 0.022†
Woody climbers	PET	1	12	25.61	< 0.022
	MAR	1	13	50.02	< 0.001
	MI	1	13	62.32	< 0.001
Ferns	PET	1	13	25.05	< 0.038

‡ using a χ^2 test. * over-dispersion is high and the *F*-test is not significant, † significant spatial structure in the residuals. For abbreviations and units of the explanatory variables see Table 1. For other abbreviations see Table 2.

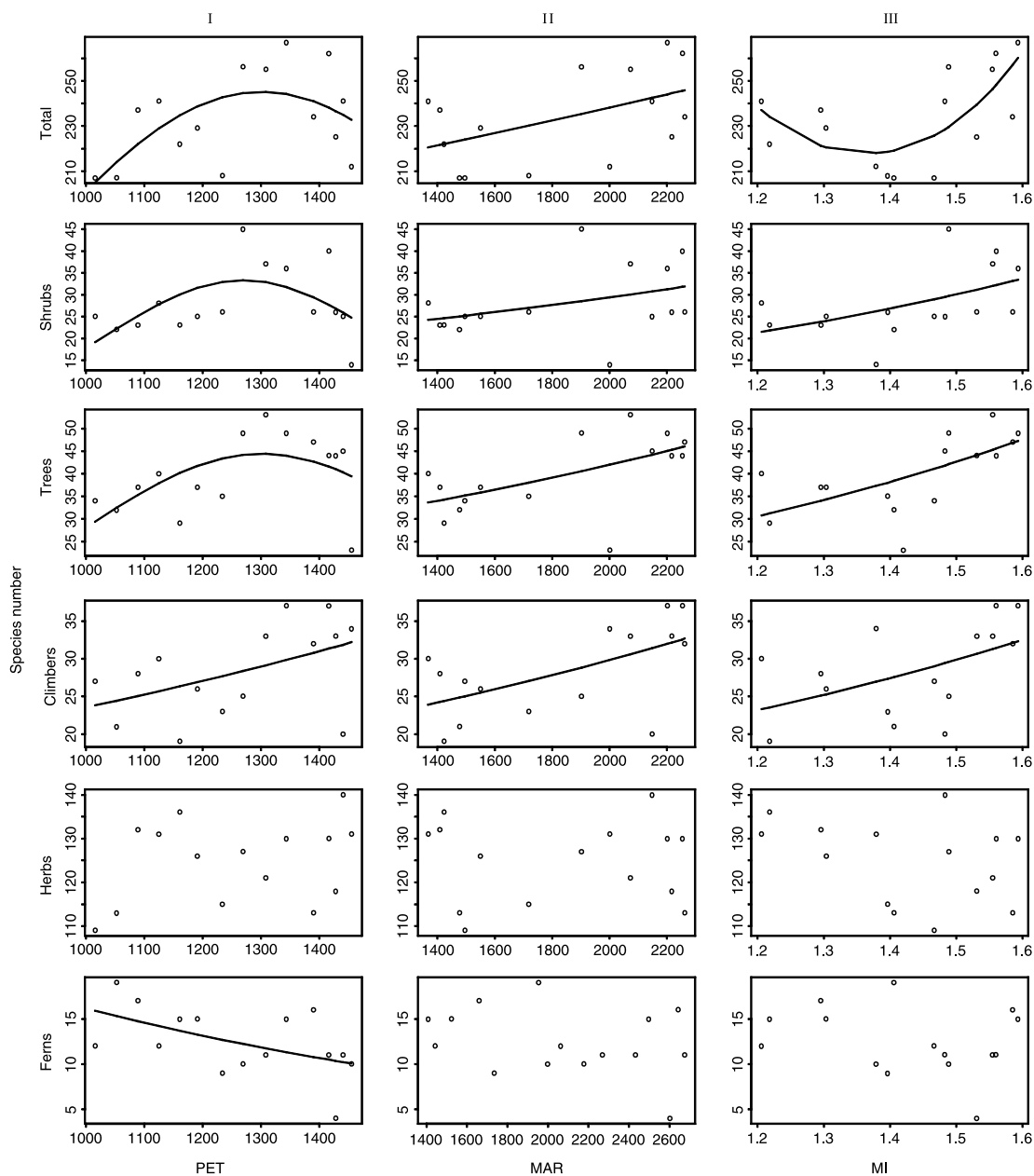


Fig. 4 The relationships between species richness of different life forms and: (I) Potential evapotranspiration in mm (PET) (II) Mean annual rainfall in mm (MAR), and (III) Moisture index (MI). The fitted lines are based on Generalized linear models with a significant χ^2 test. See Table 4 for regression details.

Climbers, including both herbaceous and woody species, have a positive log linear relationship with all variables, but the residuals of the MI-model have a significant spatial structure. Herbaceous climbers have no significant relationships with any of the climate variables. In contrast, woody climbers have positive log linear relationships with all variables, and the residuals have no spatial structure. Ferns have a negative

log linear relationship with PET, but no relationships with the moisture variables. There are no significant relationships between the climate variables and the herbaceous species groups, i.e. grasses, forbs, and total herbaceous species.

The combination of MAR and PET in the bi-variable model [richness = MAR + (PET-PET²)], was tested for all life forms. The full model was only statistically significant (Chi

Table 5 Summary of regression statistics of bi-variable models for: (a) shrubs (b) trees, and (c) woody species (shrubs + trees). The deviance explained indicates percentage of total (null) deviance. For abbreviation, and units of climate variables see Table 1. For graphical illustrations see Fig. 5

Models	Degrees of freedom	Residual deviance	%-deviance explained	P-value [‡]
Shrubs				
Null	14	31.27		
MAR	13	26.74	14.49	< 0.033*
(PET-PET ²)	12	22.22	28.95	< 0.011
MAR + (PET-PET ²)	11	11.66	62.85	< 0.001
Trees				
Null	14	25.80		
MAR	13	17.37	32.67	< 0.003*
(PET-PET ²)	12	18.60	27.90	< 0.027
MAR + (PET-PET ²)	11	8.41	67.40	< 0.011
Woody				
Null	14	50.92		
MAR	13	38.02	25.33	< 0.001
(PET-PET ²)	12	35.66	29.97	< 0.001
MAR + (PET-PET ²)	11	15.20	70.14	< 0.001

‡ using a χ^2 test. * over-dispersion is high, and the *F*-test is not significant. For other abbreviations see Table 2.

and *F*-tests) for phanerophytes, i.e. for trees and for shrubs, and for both combined (trees + shrubs) (Table 5). The over dispersion, found in the submodels for shrubs (Table 4), disappeared in the full model. The dispersion parameter is close to one and both tests are significant (Table 5). The significant spatial structure, found in the submodels for trees (Table 4), disappeared in the full model. The full model explains 63% of the total (null) deviance for shrubs, 67% for trees and 70% for the combined woody species group (Table 5).

DISCUSSION

Climatic elevation gradient of species richness

There are statistically significant relationships between species richness and the climate variables for all life forms, except for herbaceous species (Table 4, and Fig. 4). The interpretation of the elevation gradient as a climate-energy gradient is based on a strong correlation between elevation and mean annual temperature (MAT) ($r = 0.99$), where PET is linearly related to MAT (Lambert & Chitrakar, 1989) and the steepness of the regression slope depends on the season, and its lapse rate (Vetaas, 2002). Whittaker *et al.* (2001) suggest that at the macro scale spatial gradients, such as latitude, should be labelled climate gradients. This is particularly true for elevation because the temperature-elevation gradient is probably one of the most continuous ecological gradients on a macro scale (Vetaas, 2000), which together with the composi-

tional change of vegetation (i.e. coenocline) represents an ecocline (Whittaker, 1956; Whittaker & Niering, 1975; Austin, 1996). This ecocline is a complex gradient where several biotic and abiotic ecological factors correlate. Among these factors, precipitation is commonly found to have a relatively complex pattern (Lomolino, 2001) and it appears to be statistically independent of the linear change of energy along the studied gradient. The climatic-elevational gradient of plant species richness is group-specific and varies according to life forms. It is probably related to the eco-physiological properties of each life form.

Total species

Total species richness, i.e. of all life forms, has a significant hump-shaped pattern along the energy gradient (i.e. elevation). Maximum species richness occurs at optimal (1200–1300 mm) PET. The same pattern is found for flowering plants (ferns excluded) (Fig. 3 and Table 3). This is comparable with the estimates obtained by interpolation from elevation range data (Grytnes & Vetaas, 2002; Vetaas & Grytnes, 2002). The former study estimated a monotonic increasing trend of species richness from 100 to 1500 m a.s.l., and optima between 1500 and 2000 m a.s.l. Although the results reject a monotonic trend from 100 to 1500 m a.s.l., it supports an increasing trend from 100 to 800 m a.s.l. This evidence is important because the interpolation method is uncertain especially towards the edge of the gradient, where incomplete sampling may be relatively high (Grytnes &

Vetaas, 2002). Despite these uncertainties, it is empirically confirmed that there are fewer species in the subtropical lowland compared with the adjacent elevated area.

A decrease in species richness from 800 m a.s.l. down towards the subtropical lowland is counterintuitive if one considers the extension of the area where the potential regional species pool exists. The subtropical lowland of Nepal (Terai) belongs to the same geomorphological and biogeographical region as the Deccan plateau, which is an extensive plain in the north Indian subcontinent (c. 240 000 square km). Potentially, it may contribute with a large species pool to the area below 500 m a.s.l. The species pool is regarded as an important factor in determining community richness (Eriksson, 1993; Zobel, 1997). At a coarser scale one may argue that a regional species pool will influence species richness in environmentally similar areas, thus a high species richness in the lowland of Nepal might be expected due to the potentially large species pool of the Deccan plateau. However, the species pool of the extensive northern Indian plain, including Terai, is probably limited by human impact, since this area has one of the highest densities of human population in the world, and the natural vegetation has, to a large extent, been substituted by agriculture. This may explain the low number of species. Human disturbance of natural vegetation may actually increase the species richness (Huston, 1994; McKinney, 2002) if a new habitat is created and enough species are left of the original vegetation. However, the intensity of human activity in this region probably far exceeds a conjectured intermediate disturbance level at the macro scale.

The increase in species richness from the lowland up to 800 m a.s.l. is in contrast with the classical view of decreasing species richness with higher elevation (MacArthur, 1972; Brown, 1988; Begon *et al.*, 1990; Rohde, 1992; Stevens, 1992). However, Rahbek (1995) has shown that many studies have a low to mid-altitude peak in species richness (e.g. Whittaker, 1960; Shmida & Wilson, 1985; Lieberman *et al.*, 1996; Heaney, 2001; Md. Nor, 2001; Rickart, 2001; Sánchez-Cordero, 2001). Although this transect is located in the foothills of the great Himalayan range, the end point of the actual transect is located on a local mountain top (c. 1500 m a.s.l.) (Fig. 1b). Thus, maximum species richness at 800 m a.s.l. is a local mid-elevation peak. A spatial effect of conical mountain peaks is that the ground area decreases towards the peak, which reduces the probability of immigration due to lack of an adjacent species pool, which consequently leads to a reduced number of species.

The mid-elevation peak may also be a result of the intermediate location between the temperate Himalayan flora and the subtropical flora in the lowland, which increases the chances for immigration from both directions, i.e. a mass effect (*sensu* Shmida & Wilson, 1985; Grytnes & Vetaas, 2002). We argue that this is plausible even if the elevation gradient represents a vegetational continuum, i.e. coenocline (Whittaker, 1956;

see also Vazquez & Givnish, 1998 and references therein). Thus it is not dependent on discrete vegetation zones or communities that integrate in the mid-elevation zone, as suggested by Lomolino (2001) and Brown (1995, 2001). Any point on the ecocline represents a transition zone.

A positive relationship between the moisture variables (MAR and MI) and total species richness is ecologically meaningful. Higher water and optimum energy will increase photosynthesis, which leads to higher biological activities and ultimately an increase in species richness. The species richness should be greatest where energy is optimized and moisture maximized throughout the year (O'Brien, 1993, 1998; O'Brien *et al.*, 1998). Although, the intermediate peaks in species richness seem to be the most common pattern (Rahbek, 1995; Brown, 2001; Lomolino, 2001), the different pattern, observed in the present study are not surprising and presumably reflects the different eco-physiological adaptations to climate (cf. Lomolino, 2001).

Woody

The richness of shrubs and trees have the same pattern of variation as the total richness (Fig. 3). Woody species (shrubs, trees and combined) had a significant monotonic increase with rainfall and a parabolic relationship with PET in a bi-variable model (Fig. 5). This is consistent with the water-energy dynamics model for woody species richness (O'Brien, 1993, 1998). The maxima of woody species richness, and of total richness, are just above the zone of maximum precipitation (500 m a.s.l.) and the peak in the moisture index, MI (600 m a.s.l.) (Fig. 2). The peak represents the combination of optimal

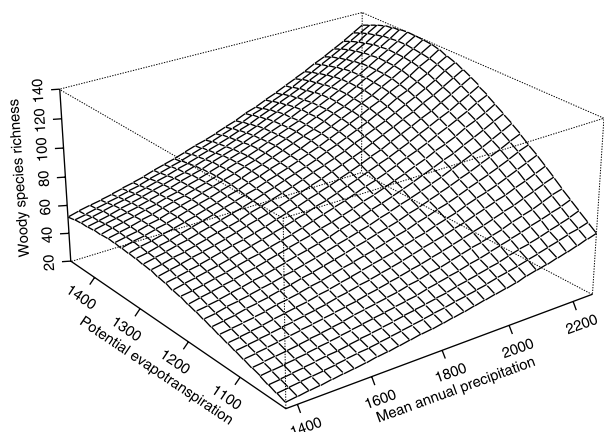


Fig. 5 The relationship between woody species richness (z-axis) and Mean annual precipitation or rainfall (MAR = x-axis), and Potential evapotranspiration (PET = y-axis). The water-energy-dynamics are expressed in a bi-variable model: Woody species richness = $MAR + PET - (PET)^2$. The fitted surface is based on Generalized linear models, for details see Table 5c.

PET (energy) and maximum moisture along the elevation gradient (cf. Brown, 2001). This is indirectly shown by the linear relationship with the moisture index derived from the Holdridge life-zone model (Holdridge *et al.*, 1971). The latter model and the water-energy dynamics model of O'Brien (1993, 1998) are both scaled for macro-ecological conditions, and it is therefore rewarding that these basic climatic variables also have strong predictive powers on a finer scale.

Climbers

Climbers, and woody climbers in particular, have a monotonic increasing relationship with PET, i.e. a decrease as elevation increases, which was also found by Vazquez & Givnish (1998) on a Mexican tropical mountain. One may hypothesize that there is a significant correlation between richness of lianas and woody species. This was partially confirmed for woody climbers ($r = 0.58$). Both groups have positive responses to MAR and MI, and they decrease towards the top of the elevation gradient, but woody species have a significant peak around 700 m a.s.l., i.e. PET = 1250–1300 mm (Figs 4I and 5). The herbaceous climbers did not respond to any of the climate variables, and there was no positive correlation with trees or shrubs. The reason for this is not obvious, but it may relate to their response to local factors as for herbaceous species in general (see below).

Herbs

The herbaceous species, in contrast to the woody species, have no relationship with any of the climate variables (Fig. 4). It was expected that the climate gradients should influence herbaceous species richness, as has been shown, e.g. by Richerson & Lum (1980). However, several studies have shown that herbaceous patterns do not run parallel to those of trees and shrubs along the elevation energy gradient (see Whittaker, 1956, 1972; Whittaker & Niering, 1965). In a study from New Zealand, Ohlemüller & Wilson (2000) found no relationship between herbaceous species richness (ground flora) and elevation. In the herbaceous group, we have included all types of herbaceous species including grasses. It is believed that grasses show weak species richness pattern along geographical gradients. However, no trend appeared when the herbaceous group was divided into grasses (37%) and forbs (63%). Although the water-energy dynamic model (O'Brien, 1993, 1998) was developed for woody plants, we did expect herbaceous species to respond to climate variables.

A weak relationship between herbaceous species and climate may relate to the dynamic attributes of herbaceous species, i.e. their shorter life span and faster phase of movement (cf. Grime, 1977). If one considers the hierarchical theory of species diversity (Whittaker *et al.*, 2001), the herbaceous

species may be relatively more influenced by local factors, such as soil conditions, disturbance, and degrees of canopy cover in the landscape (Vetaas, 1997), rather than macro scale factors.

Ferns

Ferns are the only group that display a monotonic increase from 100 to 1500 m a.s.l., as hypothesized for the flowering plants (Grytnes & Vetaas, 2002). The decreasing trend of ferns with increasing PET (energy) was expected due to the potential for excessive loss of moisture with high energy (i.e. in the lowlands). A lower diversity of ferns at low elevation and an increasing trend up to 1400–2000 m a.s.l. have been reported from several mountains, e.g. in Mexico (Tyron, 1989) and Malaysia (Md. Nor, 2001). Although the elevation of maximum species richness varied from 2300 m in New Guinea, to 1800 in the Andes, and 1300 m in Mexico (see Tyron, 1989), they all have a similar mid-elevation peak in diversity. Our study transect is located at the beginning of the Himalayan elevation gradient, and therefore the maximum richness of ferns is probably beyond the local transect top (i.e. 1500 m a.s.l.). Interpolated range data (K.R. Bhattarai & O.R. Vetaas, unpublished observation) of the total Himalayan gradient indicates a maximum at 2000 m a.s.l. Although Pteridophytes, as a group, favour the cool and moist conditions of higher elevations (Gurung, 1985), the present result is not consistent with this, as surprisingly, there is no significant relationship with MAR or MI.

The data presented herein have: (1) shown a strong relationship between climate and woody species and ferns, but not for herbaceous species, including herbaceous climbers; (2) rejected the hypothesis that species richness decreases monotonically with increasing elevation; (3) rejected the hypothesis deduced from interpolation that species richness of flowering plants has a monotonic increasing trend from 100 to 1500 m a.s.l., and replaced this with a hump-shaped or unimodal alternative hypothesis; (4) supported the hypothesis that woody species richness is a linear function of water and a parabolic function of energy; (5) supported the idea that species richness increases monotonically with increasing elevation for ferns; and (6) rejected the idea that, the subtropical lowland of Nepal (i.e. Terai) is more rich in species than the nearest elevated hills.

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BIOSKETCHES

Khem Raj Bhattarai is a doctoral student at the Department of Botany, University of Bergen. His research interest is the pattern of plant species richness along the elevation and productivity gradients of the Himalayas.

Dr Ole R. Vetaas is a vegetation ecologist at the Centre for Development Studies, University of Bergen (UoB). His research interests are diversity, succession, and spatial dynamics in extreme environments such as mountainous and arid areas. His research in the Himalayas includes disturbance and diversity in forests, climate niches of rhododendrons, and biogeographical patterns in species richness. (www.uib.no/people/nboov/biodiv.htm).