



Fern species richness along a central Himalayan elevational gradient, Nepal

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ABSTRACT

Aim The study explores fern species richness patterns along a central Himalayan elevational gradient (100–4800 m a.s.l.) and evaluates factors influencing the spatial increase and decrease of fern richness.

Location The Himalayas stretch from west to east by 20°, i.e. 75–95° east, and Nepal is located from 80 to 88° east in this range.

Methods We used published data of the distribution of ferns and fern allies to interpolate species elevational ranges. Defining species presence between upper and lower elevation limit is the basis for richness estimates. The richness pattern was regressed against the total number of rainy days, and gradients that are linearly related to elevation, such as length of the growing season, potential evapotranspiration (PET, energy), and a moisture index (MI = PET/mean annual rainfall). The regressions were performed by generalized linear models.

Results A unimodal relationship between species richness and elevation was observed, with maximum species richness at 2000 m. Fern richness has a unimodal response along the energy gradients, and a linear response with moisture gradients.

Main conclusions The study confirms the importance of moisture on fern distributions as the peak coincides spatially with climatic factors that enhance moisture levels; the maximum number of rainy days and the cloud zone. Energy-related variables probably control species richness directly at higher elevations but at the lower end the effect is more probably related to moisture.

Keywords

Nepal, Himalayas, ferns, elevation, climate, species richness, unimodal and linear responses.

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INTRODUCTION

Biologists have long recognized the striking geographical variation of species richness (von Humboldt, 1855; Wallace, 1878). Studies of several groups of organisms have identified pronounced variations in species richness along elevational gradients (Yoda, 1967; Terborgh, 1971, 1977; Hamilton, 1975; Wolda, 1987; Hawkins, 1999; Kessler, 2000, 2002; Ohlemüller & Wilson, 2000; Sánchez-Cordero, 2001; Hemp, 2002; Vetaas & Grytnes, 2002). Different historical and climatic variables have been used to explain the variation of species richness along elevational gradients (Rahbek, 1995, 1997; Vetaas, 1997; Grytnes *et al.*, 1999; Odland & Birks, 1999; Lomolino, 2001; Bhattarai & Vetaas,

2003; Grytnes, 2003a). Climatic variables influence species richness along elevational gradients for all kinds of living organisms (see Heaney, 2001; Md. Nor, 2001; Whittaker *et al.*, 2001 and reference therein). The climatic factors that vary with elevation include temperature, potential evapotranspiration (PET), length of growing season, humidity, air pressure, nutrient availability, ultraviolet radiation and rainfall (Funnell & Parish, 2001), which can all have an influence on the distribution of species along the gradient (Körner, 1999). The range margins of individual species in the gradient are determined directly or indirectly by unsuitable extremes of these climatic factors. The upper limit of a species distribution is generally thought to be determined by low temperature, quantity of snowfall, length

of growing period, and wind intensity, whereas at the lower end the range limit may be determined by a combination of climatic and biotic factors (MacArthur, 1972).

The processes that influence the species richness across the gradient may differ among the taxa (Ricklefs, 1987, 1989). The majority of elevation studies have focused on woody plants (e.g. Yoda, 1967; Kitayama, 1992; Liberman *et al.*, 1996), although the majority of plant species in forests belong to non-tree life forms (Gentry & Dodson, 1987). The ferns belong to a rather primitive group of vascular plants but contribute significantly to the number of species in the flora of tropical and sub-tropical mountains. In contrast to many woody plants, ferns are dispersed by means of small spores and establish new populations in distant localities, they exhibit lower endemism, and less frequent speciation, they have a mostly herbaceous perennial growth form (a few are annuals and or tree-like), need moisture, and they have a long evolutionary history (Smith, 1972; Page, 1979; Kato, 1993). Because of these unique features, patterns of fern and flowering plant richness along an elevational gradients may not be concurrent (Bhattarai & Vetaas, 2003). Although there are many studies related to fern ecology, relatively few studies have addressed the change of diversity along elevational gradients (but see for e.g. Kessler, 2000 in the Bolivian Andes, Kitayama, 1992; Md. Nor, 2001 on Mt Kinabalu, and Hemp, 2002, on Mt Kilimanjaro).

Studies of variation in richness from sea level to mountain summits are important to find out patterns across the whole range of gradients (Lomolino, 2001). A study conducted covering half a gradient may not reflect the total patterns along the gradient. Thus, this study by analysing the whole, as well as two sub-gradients, aims to show how patterns may vary if one considers half of the gradient rather than whole. The Himalayas contain the highest mountains in the world with a diverse range of eco-climate zones (Dobremez, 1976). Elevational gradients, such as the Himalayas, can serve as an excellent system to evaluate ecological and biogeographical theories of species richness and their relationships to climate (Körner, 2000).

Using standardized sampling along an elevational gradient (100–1500 m), Bhattarai & Vetaas (2003) found a positive monotonic pattern for ferns and a unimodal pattern for flowering plant species richness. Therefore, in this study we address the issue of why ferns do not have the same pattern as flowering plants. The richness of ferns and fern allies is evaluated to generate hypotheses about the potential causal factors that determine variation in fern richness along the elevational gradient, and explore operational different effects of the same factor at the upper and lower end of the gradient. Thus, this study specifically aims to: (1) explore the variation in fern species richness along an elevational gradient, extending from 100 to 4800 m and along two sub-gradients (100–2000 and 2000–4800 m), (2) show how climatic factors may explain the variation in species richness along the whole and sub-gradients and (3) compare fern richness with angiosperm species richness.

MATERIALS AND METHODS

Biogeographical location of the study area and its vegetation

The study area covers the central Himalayas, Nepal, (80°04'–88°12' E and 26°22'–30°27' N), which is c. 900 km long (Fig. 1a). The Himalayas consist of three ranges running south-east to north-west in Nepal: Siwalik range (maximum 1000–1500 m), Mahabharat range (maximum 2700–3000 m), and great Himalayas (5000–8000 m) (Hagen, 1969; Manandhar, 1999) (Fig. 1b).

The Himalayan elevational gradient is the longest bioclimatic gradient in the world extending from c. 60 to more than 8000 m within 150–200 km, south to north, and comprises tropical/subtropical, temperate, sub-alpine and alpine climatic zones. There is a tropical/sub-tropical zone to 1000 m, dominated by *Shorea robusta*, *Adina codifolia*, *Dalbergia sissoo* and species of *Terminalia*. In the warm temperate zone (1000–2000 m) the forest is dominated by a mixture of *Schima wallichii*, *Castanopsis indica* and *Pinus roxburghii*. Some patches of tree fern (*Cyrtosperma spinulosum*) also occur in this zone. In the cool temperate zone (2000–3000 m), the forest is dominated by laurel, oak and *Rhododendron*. The sub-alpine zone (3000–4000 m) is dominated by *Betula utilis* and coniferous forest. The upper elevation limits for *Abies spectabilis*, *Pinus wallichiana*, and *B. utilis* are 4000–4300 m. In the western part of Himalaya, the timberline is slightly lower than the eastern part (Mani, 1978). In the alpine zone above the timberline, the vegetation is dominated by shrubs (*Rhododendron*, *Juniperus*, *Rosa* and *Hippophae*) and alpine meadows. Ferns are found from below 100–4800 m in Nepal (Thapa, 2002).

Data sources

We used the elevational range data from 'An enumeration of pteridophytes of Nepal' (Iwatsuki, 1988), where both ferns and fern allies (*Lycopodium*, *Selaginella* and *Equisetum*) are included. This source provides elevational limits for 228 taxa, and there are an additional 65 species whose range is crudely indicated by low, middle and high elevation. For these latter taxa we used range data given in Gurung (1991). Both sources are based on extensive botanical surveys covering all phytogeographical zones of Nepal and examination of herbarium specimens deposited in major herbaria of Himalayan plants. We also derived epiphytic fern species richness using the same methods and sources. To show the relationship between epiphytic ferns and tree species richness, we derived tree species data from Press *et al.* (2000). The tree species were also interpolated using the same method as above. The taxonomy and nomenclature of ferns follow Iwatsuki (1988).

We divided the elevational gradient between 100 and 4800 m into 48, 100-m elevation intervals. A species was defined as present in every 100-m interval between its upper and lower elevation limits. For example, a species with its

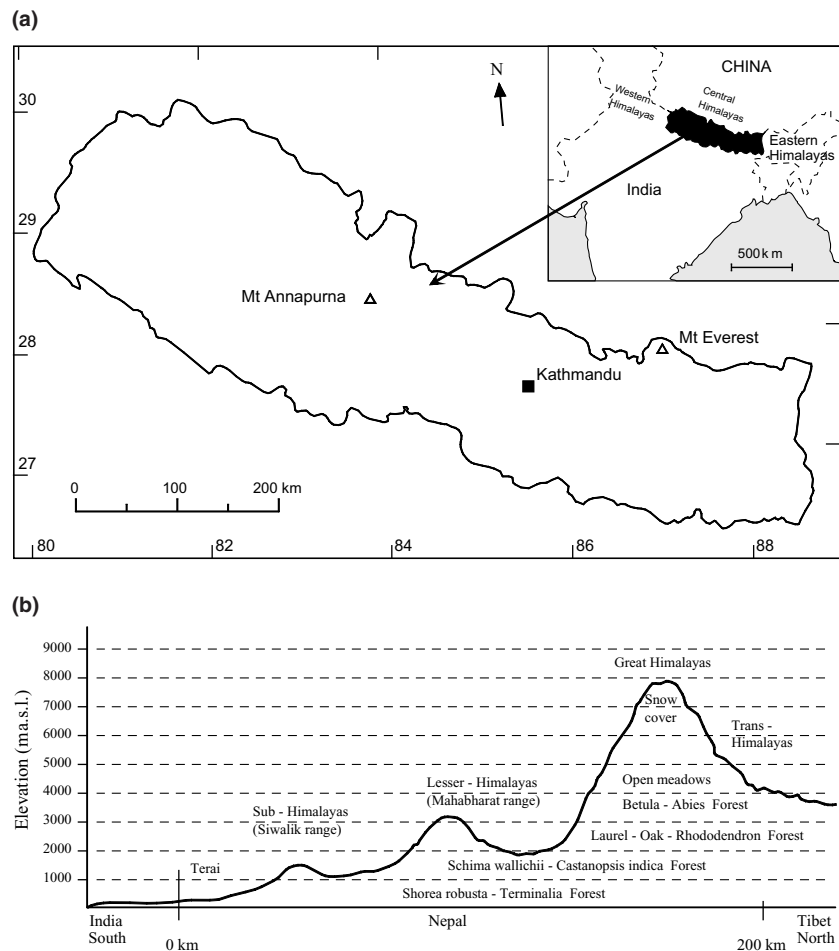


Figure 1 (a) Location of central Himalayas, Nepal, (b) Schematic cross-section of central Himalayas, Nepal, from south to north showing the four mountain systems of Himalayas and the corresponding vegetation types.

elevation limit between 1260 and 1670 m is then present in the 1300, 1400, 1500, 1600 and 1700 m elevation bands (see Patterson *et al.*, 1996, 1998; Rahbek, 1997; Fleishman *et al.*, 1998; Brühl *et al.*, 1999; Grytnes & Vetaas, 2002). This gives an estimate of gamma diversity, defined as the total richness of an entire elevation zone (*sensu* Lomolino, 2001) (originally introduced by Whittaker, 1972; cf. Vetaas & Grytnes, 2002). We use the term species richness (Peet, 1974) or fern richness (including fern allies), as the number of fern species present in each 100-m band, because the fern diversity is often used for indices combining richness and evenness.

Climate and climatic variables

The climate of Nepal falls within the monsoon system of the Indian subcontinent, with dry periods in the winter and wet periods in the summer. More than 80% of the rainfall occurs during the four summer months (June–September). Mean annual temperature at 100 m is 25 °C and decreases by 0.53 °C (adiabatic lapse rate) per 100-m increasing elevation. Cloud formation is a decisive factor for the vegetation of Nepal (Beug & Miehe, 1999). The lower condensation point of the clouds is around 2000 m. Cloud formation starts above c. 1400 m and appears frequently at c. 2000 m in the lesser

Himalayas, whereas in the greater Himalayas it is normally between 2500 and 3200 m (Dobremez, 1976). The lower cloud zone, which starts c. 1400 m is not persistent and disappears after a few hours but the upper cloud zone is more persistent.

We used climate data from 97 climate stations located from 72 to 4091 m, with records covering 1971–96 (Department of Hydrology and Meteorology, Government of Nepal). We considered both energy-related and moisture-related variables as potential explanatory factors for variation in fern richness. We estimated total number of rainy days, length of growing season, and mean annual rainfall per 100-m elevation band. We did not find any rainfall patterns along the increasing elevational gradient so rainy days are used as a moisture variable, but we retained mean annual rainfall in the calculation of the moisture index (MI) (see below).

Annual PET is used as a surrogate of energy (O'Brien, 1998). PET is expressed as mm year⁻¹ and is an estimate of the potential amount of water released through surface evaporation and transpiration from homogeneous covered vegetation that is well supplied with water (Currie, 1991). PET and the MI were calculated using the formula of Holdridge *et al.* (1971), [PET = mean annual bio-temperature (i.e. temperature > 0 °C) × 58.93 and MI = PET/mean annual rainfall]. For simplicity MI was inverted, where values below 1 indicate a

negative water balance, whereas values above 1 indicate a positive water balance (Vetaas, 2002). Length of the growing season was crudely estimated by assuming that there are 365 growing days at 1200 m (no frost days) and no growing period above 5500 m, which has a mean summer temperature below 4 °C. Plants usually respond to growing season when total summer temperatures >5 °C (Woodward, 1987). There are frost sensitive plants, like papaya and banana successfully growing up to 1200 m and there are a few plants above 5500 m but no ferns.

The climate stations are not uniformly distributed, and some elevation intervals lack stations, e.g. 600–800, 2800–3000, 3100–3400, 3500–3800 and 3900–4100 m. In these bands mean annual rainfall and rainy days were interpolated from the mean value of the nearest adjacent upper and lower climatic station's record. Variables in each 100-m band above 4100–4800 m were extrapolated by generalized additive models (GAM) (Hastie & Tibshirani, 1990), with 4 d.f., as the precipitation or rainy days are not assumed to have a linear relationship with elevation. In the GAM, elevation bands having more stations are assigned higher weights to estimate the respective contribution of stations in each band. Climatic trends along the elevational gradient are shown in Fig. 2. The mean annual temperature shows the same pattern as PET (cf. above), but we have selected PET as an explanatory variable because it has more ecological meaning; it is a function of several climate variables, which indicate the environmental demands for water (O'Brien *et al.*, 1998). Both are related to ambient energy.

Species–area relationship

Species numbers tend to increase as a function of area (e.g. Gleason, 1922; Rahbek, 1997; Rosenzweig, 1997), but the different 100-m bands do not contain equal areas because of the complex topography of the Himalayas along the elevational gradient. Estimates of the areas in each 100-m band are not available, but area is estimated for each 500-m elevation bands by the International Center for Integrated Mountain Development (ICIMOD, Katmandu) based on digitized maps. These area estimates were correlated with fern species richness in each 500-m elevation band (Vetaas & Grytnes, 2002), and the relationships between elevation, area, and fern richness are examined by scatter plots.

Statistical analysis and autocorrelation

Initially, we used the elevational gradient as an explanatory variable and species richness as the response variable. As indicated above, all energy-temperature variables have simple linear relationships with elevation (Fig. 2). Although the climate factors are highly correlated with species richness along the total gradient, we assume that their operational effects may differ at opposite ends of the gradient. Temperature, for instance, may cause lethal frost at high elevations whereas it may regulate moisture availability at the lower end. Comparing the richness pattern at two extremes of the

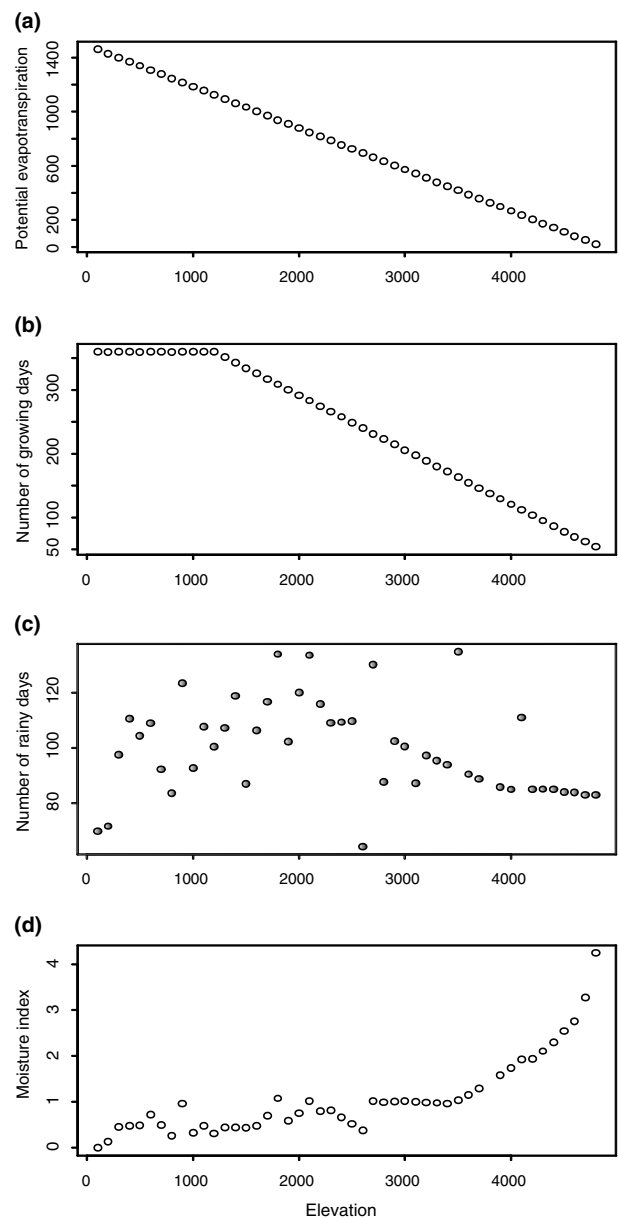


Figure 2 Scatter plot showing the relationship between elevation (m a.s.l. = x-axis) and (a) potential evapotranspiration (PET), (b) length of growing season i.e. number of growing days, (c) number of rainy days per year, (d) moisture index (in log scale) along the y-axis.

gradient may allow a finer resolution of the causal factors on species richness relationships. Therefore, we divided the total gradient in two sub-gradients from 100 to 2000 m and from 2000 to 4800 m and analysed them separately as well as the total gradient.

We used a generalized linear model (GLM; McCullagh & Nelder, 1989; Dobson, 1990) to relate species richness with elevation and climatic variables. GLM is a popular technique used to relate species richness to climate variables (e.g. Austin & Cunningham, 1981; Pausas, 1994). Species richness is count

(discrete) data and may have a Poisson distribution error (McCullagh & Nelder, 1989), which requires a logarithmic link. The regression models were also checked by using an identity link function (assuming a normal distribution of errors). The residuals were examined by drawing Q–Q diagnostic plot (Crawley, 1993, 2002; Hastie & Pregibon, 1993; Quinn & Keough, 2002). We found that Poisson models gave a better fit than Gaussian models.

We tested each variable separately. The models were checked with up to third-order polynomials. The first, second and third order polynomials were tested against null models and against each other. The adequacy of the fitted statistics was confirmed by plotting standardized residuals against the fitted values, and with normal probability plots (Crawley, 1993).

Fern richness in each 100-m interval 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. This spatial autocorrelation inflates Type-I error in statistical analyses (Diniz-Filho *et al.*, 2003), which can be a problem when explicit causal factors are being tested (Legendre, 1993; Lennon, 2000). The estimation of species richness by interpolation is a relatively weak technique compared with direct sampling, and it will enhance the autocorrelation as we assumed that ferns were present in all elevation zones between their range limits, thereby ignoring any disjunctions in their distribution along the elevational gradient (Vetaas & Grytnes, 2002). Our aim is to generate hypotheses about how climatic factors influence fern richness, thus we do not aim to predict a certain number of fern species at given value of any explanatory variables. To evaluate our hypothesis we checked for autocorrelation both in our raw data and in the residuals from the species–climate regression models (Lichstein *et al.*, 2002). We used Moran's I coefficient to compute the correlograms, which is the most commonly used method to check autocorrelation in species richness analyses (Diniz-Filho *et al.*, 2003). Moran's I

coefficient has a value near zero when there is no spatial autocorrelation in the data. Positive and negative Moran's I coefficients indicate positive and negative autocorrelation, respectively (Cliff & Ord, 1981; Legendre, 1993; Lichstein *et al.*, 2002; Diniz-Filho *et al.*, 2003). We evaluated our models using *F*-tests, because they are more robust when there is over- or under-dispersion in the model (Hastie & Pregibon, 1993). We used S-plus (version 4.5, MathSoft, Inc., Seattle, WA, USA) for all regression analyses.

RESULTS

Pattern of species richness along the elevational gradient

The ferns and allied genera are distributed between 60 and 4800 m in Nepal. There are a total of 293 species, 95 genera and 35 families. The most species-rich families are the Athyriaceae and Dryopteridaceae. There are only 16 species above the forest-limit ecotone, i.e. above 4000–4300 m, representing 11 genera and three families.

The relationship between species richness and elevation is unimodal, as indicated by a statistically significant second-order term in GLM (Table 1). Maximum fern richness is observed at *c.* 2000 m (Fig. 3c). The relationships between fern richness and elevation when divided in to two gradients from 100–2000 and 2000–4800 m, have monotonically increasing and decreasing trends, respectively. Total fern species richness and epiphytic fern richness are strongly correlated ($r = 0.99$). Epiphytic fern richness also peaks at 2000 m (Fig. 3d). There is a significant correlation between epiphytic fern and tree species richness ($r = 0.66$) and total fern and tree species richness ($r = 0.67$). Area linearly decreases along the increasing elevational gradient in Nepal ($r = -0.83$). The correlation between fern richness and area is not significant (Fig. 3b), and maximum fern richness is not occurring below 1000 m with the largest available area.

Table 1 Summary of regression statistics for the species richness relationship between explanatory variables along the whole elevational gradient and two sub-gradients. The numbers 1, 2 and 3 indicate first, second and third order polynomials. The deviance explained indicates percentage of null deviance

Predictors	Range of gradient (m a.s.l.)	GLM order	d.f.	%-Exp. Dev.	<i>P</i> (<i>F</i>)
Elev./PET	100–4800	2	45	98.67	$P < 0.001$
	100–2000	1	18	93.31	$P < 0.001$
	2000–4800	1	27	92.69	$P < 0.001$
Gr. days	100–4800	2	45	87.74	$P < 0.001$
	100–2000	1	18	58.71	$P < 0.001$
	2000–4800	1	27	92.62	$P < 0.001$
R. days	100–4800	1	46	27.15	$P < 0.001$
	100–2000	1	18	27.64	$P < 0.001$
	2000–4800	1	27	27.71	$P < 0.002$
M. index	100–4800	3	44	52.52	$P < 0.015$
	100–2000	1	18	17.42	$P = 0.055$
	2000–4800	1	27	79.12	$P < 0.001$

GLM, generalized linear model; PET, potential evapotranspiration; d.f., degree of freedom; Exp. Dev., explained deviance; *P* (*F*), probability in *F*-test; Elev., elevation; Gr. days, number of growing days; R. days, number of rainy days; M. index, moisture index.

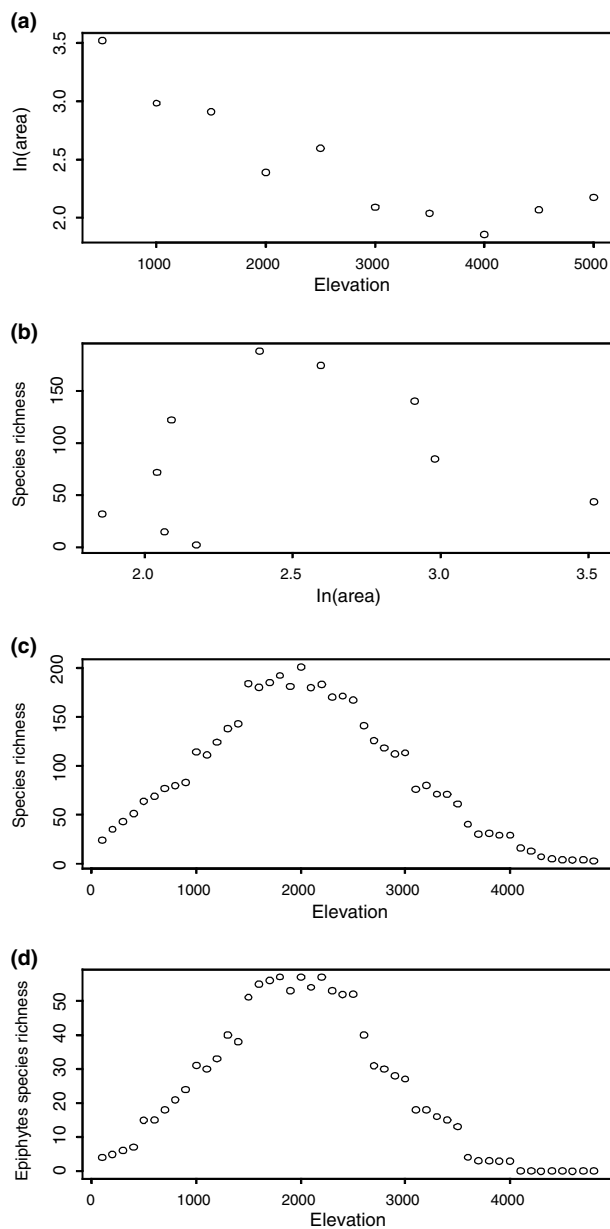


Figure 3 Scatter plots showing the relationship between: (a) area in log scale (1000 km^2 , y -axis) and elevation (x -axis), (b) species richness (y -axis) and area in log scale (1000 km^2 , x -axis), (c) total fern species richness (y -axis) and elevation (x -axis), and (d) epiphytic fern richness (y -axis) and elevation (x -axis).

Patterns of richness and climate

The relationships between the climatic variables and fern richness are shown in Fig. 4 and Table 1. In general, species richness has a unimodal relationship with energy-related variables, i.e. PET and length of growing season, and a log-linear relationship with the number of rainy days (moisture-related variable) (Table 1). The richness trend along PET is the same as elevation because both variables are highly correlated ($r = 0.99$) (Fig. 2a). The optimum PET values for fern richness is between 800 and 1000 mm (Fig. 4a), which appears

around 2000 m. Fern richness monotonically decreases towards higher (lowland) and lower (highland) values of PET. Fern richness has a unimodal relationship along the length of growing season gradient (Fig. 4b), and a log-linear relationship along the total rainy day gradient. It also has a log-linear relationship along the two sub-gradients (100–2000 and 2000–4800 m) with respect to number of rain days (Fig. 4c & Table 1). The relationship between fern richness and MI has a unimodal trend along the total gradient, and a negative log-linear trend above 2000 m. Below 2000 m there is no significant trend (Fig. 4d & Table 1).

The correlogram for fern species richness along elevation (Fig. 5a), indicates that richness is positively autocorrelated up to *c.* 1200 m, followed by a continuous decrease in Moran's I coefficients up to *c.* 3200 m, at which point there is a negative autocorrelation coefficient. Above *c.* 3200 m a strong positive autocorrelation reappears. There is no spatial structure in the residuals when PET is used as an explanatory variable in the regression models (Fig. 5b), but there is strong spatial structure in the residuals when fern richness is regressed against number of growing days, rainy days, and MI (Fig. 5c–e).

DISCUSSION

Mid-elevation peak in species richness

Fern richness varies strongly with elevation in Nepal as has been observed for flowering plants (Grytnes & Vetaas, 2002). Fern richness has a pronounced peak at 2000 m and decreases in both directions. The peak in richness is approximately in the middle of the gradient (100–4800 m), and such mid-elevation peaks in fern richness have also been found in other regions (e.g. Parris *et al.*, 1992; Wood *et al.*, 1993 in Borneo, and Kessler, 2000 in Bolivian Andes, Md. Nor, 2001 on Mt Kinabalu; Hemp 2002 on Mt Kilimanjaro).

Some authors (e.g. Colwell & Hurtt, 1994; Grytnes & Vetaas, 2002) have argued that the mid-elevation peak in species richness may be caused by hard boundaries present at both ends of the elevational gradient. The biological mechanisms involved are probably related to dispersal constraints, where mass effect (Shmida & Wilson, 1985) or source-sink dynamics (Pulliam, 1988) offer an explanation. Grytnes (2003b) proposed that, sink populations are commonly established from source populations within the domain if ecological conditions are similar. This model highlights that mid-elevation habitats have a relatively higher diaspore input than areas close to the endpoints of the elevational gradient, which mostly have diaspore input from one direction only.

The upper limit for vascular plants is at around 6000 m, and its influence on ferns is obviously non-existent as ferns and fern allies have an upper limit at 4800 m in the Himalayas. Only 1% of fern species are found in the alpine zone; none of the species are obligate alpinists, and only three species [*Cystopteris sudetica* A. Br. et Milde, *Polystichum lachenense* (Hook.) Bedd. and *Athyrium wallichianum* Ching] have been

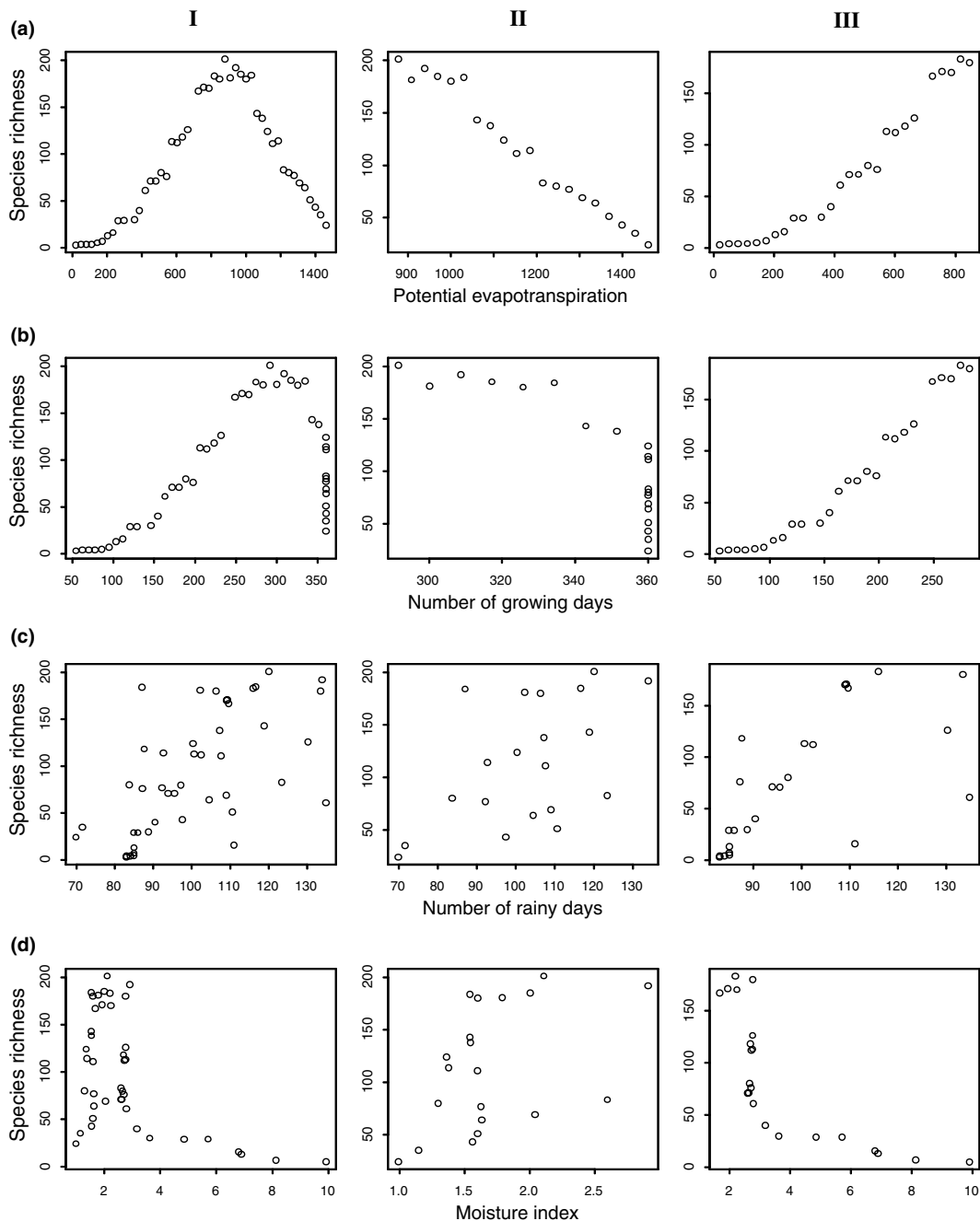


Figure 4 Scatter plots show the relationship between species richness (y -axis) and different explanatory variables: (a) potential evapotranspiration, (b) number of growing days, (c) number of rainy days, and (d) moisture index (x -axis): (I) whole elevation gradient 100–4800 m a.s.l. (II) lower sub-gradient, 100–2000 m a.s.l. and (III) upper sub-gradient 2000–4800 m a.s.l.

found up to 4800 m (the highest limit of distribution reported). This suggests that ferns in the alpine environment are mainly sink populations of sub-alpine species, which can barely tolerate the harsh and stressful open alpine habitat. Trees provide shelter against desiccation and create suitable habitat for ferns, which explains the strong correlation between trees and fern species richness. As one-third of Nepalese ferns are epiphytes (Gurung, 1985), absence of trees as a habitat and

microclimate moderator explains the decrease beyond the tree limit.

We attempted to avoid the effect of hard boundaries by discarding 700 m from both ends of the gradient, but the unimodal pattern did not disappear but it distorted the shape of the curve. This may indicate that the unimodal pattern is primarily caused by climatic factors rather than by hard boundaries (Hawkins & Diniz-Filho, 2002).

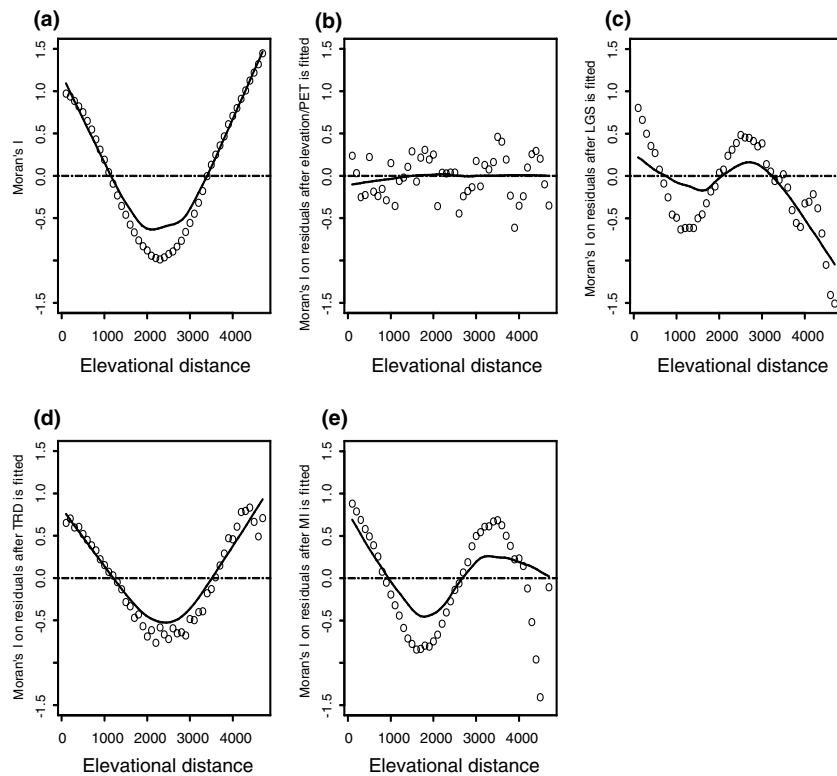


Figure 5 Spatial correlograms (whole gradient) for (a) species richness (raw data), for residual models (b) elevation/potential evapotranspiration, (c) length of growing season (LGS) i.e. number of growing days, (d) total number of rainy days (TRD), and (e) moisture index (MI). The fitted solid line is less smoother.

The amount of area decreases with increasing elevation in Nepal (Fig. 3a). If we considered species–area relationships, more species are expected in the lower part of Nepal because of the larger area available for species (Rosenzweig, 1997). This study shows that the 2000 m peak of maximum richness is not caused by the area effect, which agrees with the results from flowering plants (Vetaas & Grytnes, 2002). Our result is consistent with the argument of Lomolino (2001), that the relationship between species richness and area along an elevational gradient is an exception to the general area–species richness pattern. This may relate to the fact that the two-dimensional representation of area is not a good estimate of the actual available surface in mountainous terrain (Vetaas & Grytnes, 2002), which is better estimated as volumes (Rahbek, 1997).

Incomplete sampling at the extreme ends of the elevational gradient may cause spurious richness patterns (Lomolino, 2001). Plant exploration at high elevation is difficult compared with the lowland, and may cause biased representation of the species elevation ranges. The situation in Nepal is, in practice, rather different, as most plant expeditions have focused on the higher Himalayan Mountains rather than the tropical/sub-tropical lowlands because the main attraction is the Himalayan plants (Rajbhandari, 1976). The small number of species found in the lowlands might be due to poor sampling and habitat loss, as samples taken along a sub-tropical elevational gradient showed a clear decrease of ferns towards the lowlands (Bhattarai & Vetaas, 2003). Major deforestation in the lower part of Nepal started after the

control of Malaria, but several plant-hunting expeditions were undertaken prior to this, and therefore, the low fern richness observed here is not primarily caused by habitat loss, but may be due to climatic conditions.

In another interpolation study, covering the entire Himalayan elevational gradient (Grytnes & Vetaas, 2002), flowering plant species richness was found to peak between 1500 and 2500 m and a plateau was observed between 3000 and 4000 m. Ferns have a much more pronounced peak at 2000 m (Fig. 3c), compared with flowering plants and do not show any plateau along the gradient. The clearer peak of fern richness may be due to more specific climatic and ecological requirements of ferns compared with the composite group of flowering plants.

Climate variables and species richness

Energy

The PET explains more than 98% of deviance in fern richness, and the unimodal model has no spatial structure left in the residuals. The maximum fern richness is found between PET values of 800–1000 mm. This is consistent with an empirical study along an elevational gradient in Nepal, where fern richness decreased when PET exceeded 1000 mm. In the same study, flowering plants still increased above this range and decreased when PET exceeded 1250–1300 mm (Bhattarai & Vetaas, 2003). This indicates that ferns need more moisture than flowering plants. Hoffman *et al.* (1994) also reported similar negative trends at higher PET.

Both ends of the gradient are constrained by PET. There is an excessive loss of moisture because of high PET towards the lower end of the gradient, which may limit fern richness. Poorly controlled evaporative potentials to counter high rates of water loss characterize much of the life cycle of the majority of ferns (Page, 2002). Fern richness at upper end of the gradient is constrained by low energy associated with the lethal effects of frost. The length of growing season decreases by c. 8.5 days per 100 m, and generates a time constraint for ferns to complete their life cycle and may in part cause the monotonic decrease in fern richness above 2000 m (Fig. 4b). The length of growing season explained about 81% of fern richness, but the model is weak because there was a significant spatial structure left in the residuals.

Moisture variables

The relationship between the number of rainy days and elevation is unimodal with the maximum number of rainy days at 2000 m (Fig. 2c). The significant positive log-linear relationship between species richness and the number of rainy days was expected as free water is essential for reproduction by free-swimming motile antherozoides (Page, 2002). The high moisture conditions at 2000 m are also associated with the presence of the cloud zone, where large amount of water is deposited directly onto vegetation from clouds and light mist; known as horizontal precipitation or cloud stripping (Vetaas, 1993; Hamilton *et al.*, 1994). In addition it leads to reduced sunlight and reduced evapotranspiration (Hamilton *et al.*, 1994) and increased atmospheric humidity (Bruijnzeel & Veneklaas, 1998), which may facilitate high species richness (Vetaas, 1993; Falkenberg & Voltonilini, 1994; Rahbek, 1995). Maximum epiphytic fern richness (Fig. 3d) occurs at the same 2000 m also supports the maximum availability of moisture.

Water and energy interaction

Interaction of water and energy is crucial for biological activities and species richness (O'Brien, 1993, 1998; Whittaker & Field, 2000). One should expect a linear increase of ferns with increasing MI (Rainfall/PET). Instead there is no pattern below 2000 m, and a negative trend above 2000 m. This is probably caused by very high MI values at higher elevations (Fig. 2d), where there is plenty of water but only for a short growing season (cf. above). For the rest of the year, the moisture is tied up as snow, and hence largely unavailable to plants. It makes ecological sense that maximum fern richness at 2000 m is related to maximum availability of moisture, but all regression models including moisture variables have autocorrelated residuals. Thus the hypothesis that moisture controls the fern richness is not strong, especially because they are not based on real sampling (cf. Haining, 1990). There is also big variation in number of rainy days even in same elevation band, which is probably more pronounced than the variation in temperature within the same elevation band. PET is, statically, the best explanatory variable, but the ecological

effect of PET is probably in part a result of its influence on moisture availability and length of growing season.

In summary, the data presented here have: (1) shown strong relationships between climatic variables and fern richness along the Himalayan elevational gradient, (2) allowed us to reject the argument that ferns richness has a monotonic increasing relationship along the elevational gradient and replaced this with an alternative unimodal hypothesis, (3) helped to establish a hypothesis that ferns and flowering plants have a different optimum interval with respect to PET gradient as they have different moisture requirements and (4) supported the idea that the high mountains of Himalayas are richer in fern species than the lower plains. However, these hypotheses are based on interpolated climatic and species data, and therefore need to be verified with real sampling from fixed sample plots with measured climatic variables.

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