WILEY

Distribution of Vascular Plant Species Richness and Endemic Richness along the Himalayan Elevation Gradient in Nepal
Author(s): Ole R. Vetaas and John-Arvid Grytnes
Source: *Global Ecology and Biogeography*, Vol. 11, No. 4 (Jul., 2002), pp. 291-301
Published by: Wiley
Stable URL: https://www.jstor.org/stable/3182698
Accessed: 07-01-2019 15:01 UTC

Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal

OLE R. VETAAS and JOHN-ARVID GRYTNES*

Centre for Development Studies, University of Bergen, Stroemgaten 54, N-5007 Bergen. Norway, E-mail: ole.vetaas@bot.uib.no
*Department of Botany, University of Bergen, Allegaten 41, N-5007 Bergen, Norway

ABSTRACT

Aim Species richness and endemic richness vary along elevation gradients, but not necessarily in the same way. This study tests if the maxima in gamma diversity for flowering plants and the endemic subset of these plants are coherent or not.

Location The study was conducted in Nepal, between 1000 and 5000 m a.s.l.

Methods We used published data on distribution and elevational ranges of the Nepalese flora to interpolate presence between maximum and minimum elevations. Correlation, regression and graphical analyses were used to evaluate the diversity pattern between 1000 and 5000 m a.s.l.

Results The interval of maximum species endemic to Nepal or the Himalayas (3800–4200 m) is above the interval of maximum richness (1500–2500 m). The exact location of maximum species density is uncertain and its accuracy depends on ecologically sound estimates of area in the elevation zones. There is no positive statistically significant correlation between log-area and richness (total or endemic). Total richness is positively correlated with log-area-adjusted, i.e.

estimated area adjusted for the degree of topographic heterogeneity. The proportion of endemic species increases steadily from low to high elevations. The peak in endemism (*c.* 4000 m) corresponds to the start of a rapid decrease in species richness above 4000 m. This may relate to the last glacial maximum (equilibrium line at *c.* 4000 m) that penetrated down to 2500–3000 m. This dynamic hard boundary may have caused an increase in the extinction rate above 4000 m, and enhanced the probability of isolation and facilitated speciation of neoendemics, especially among genera with a high proportion of polyploids.

Main conclusions The results reject the idea of corresponding maxima in endemic species and species richness in the lowlands tentatively deduced from Stevens' elevational Rapoport effect. They confirm predictions based on hard boundary theory, but hard-boundaries should be viewed as dynamic rather than static when broad-scale biogeographical patterns with a historical component are being interpreted.

Key words elevational gradient, endemicity, glaciation, hard boundaries, isolation, polyploidy, speciation, species diversity.

INTRODUCTION

Biogeographical variation in species richness and endemic richness is critical to our understanding and conservation of biological diversity. Areas with high species richness may also have a high number of endemic species, but not necessarily in a coherent pattern (Huston, 1994; Whittaker *et al.*, 2001). The most characteristic centres of endemism are generally thought to be isolated oceanic islands (Williamson, 1981), e.g. Hawaii (Carlquist, 1974), New Zealand (Raven &

Axelrod, 1978) and the Canary Islands (Kunkel, 1992; cf. Hobohm, 2000). Massive topographic relief can, potentially, provide a similar barrier that inhibits gene flow and facilitates speciation (Brown, 2001). However, hot-spots of endemic plants are found both in rather flat areas, e.g. Texas and northern Florida, and in areas with high topographic relief (e.g. Andes) (Gentry, 1986). In mountainous areas, such as the Himalayas, the maximum number of endemic species is expected to occur at high elevations, due to isolation mechanisms (Shrestha & Joshi, 1996).

The central problem in all biogeographical analyses is that that the same pattern may result from several different processes (Brown, 2001) and there is also a general failure to distinguish between historical factors that relate to endemism

Correspondence: Ole R. Vetaas, Department of Botany, University of Bergen, Allégaten 41, N-5007 Bergen, Norway, E-mail: ole.vetaas@bot.uib.no

or distinctiveness and more contemporary factors related to species richness (Whittaker *et al.*, 2001). Area is a principal factor in all species richness analyses (Rosenzweig, 1997; Whittaker *et al.*, 2001) and, in general, it may decline with increasing elevation (Körner, 2000; Lomolino, 2001). However, the area available for plants on high mountains is not constant through time. Glaciation during the Quatenary has, in a long-term perspective, affected the available area at high elevation and subsequently may have controlled variation in total plant species richness as well as the degree of isolation and thereby the extent of endemism.

Species richness is generally thought to decrease with elevation (e.g. Stevens, 1992; Brown & Lomolino, 1998). Rahbek (1995), however, presented a critical review of the literature, and showed that approximately half of the studies had a mid-altitude peak in species richness (see also: Whittaker, 1960; Shmida & Wilson, 1985; Lieberman *et al.*, 1996; Heaney, 2001; Md. Nor, 2001; Rickart, 2001; Sánchez-Cordero, 2001). It has been demonstrated recently that a mid-elevation peak in species richness may result from hard boundaries (Colwell & Lees, 2000). Hard boundaries are defined in relation to the degree of resistance to dispersal and survival (Colwell & Hurtt, 1994; Colwell & Lees, 2000). This theory predicts that total species richness will have a peak close to the mid-elevation. The hard boundary theory also predicts that wide-ranging taxa are more likely to show a mid-elevation peak than narrow-ranging taxa, as the latter are assumed to be more influenced by environmental and historical factors (Colwell & Lees, 2000). Because the majority of the endemic species in the Nepalese Himalayas have a very narrow range (Shrestha & Joshi, 1996), one may hypothesize that the peaks for species richness and endemic richness are not necessarily coherent.

An alternative prediction can tentatively be deduced from Stevens's (1992) theory on Rapoport's rule (Rapoport, 1982) and its application to elevation gradients, i.e. Stevens' elevational Rapoport effect. Stevens (1992) showed that maximum richness is often found towards the lower end of elevation gradients, consistent with an elevational Rapoport effect. This theory assumes that the average range size increases with increasing elevation, thus species with a narrow range are more likely to be found at lower elevations. Because many endemic species have narrow ranges, one might expect that they have higher numbers in the tropical lowlands coherent with maximum richness.

We used published data on elevation ranges to interpolate gamma diversity (*sensu* Lomolino, 2001), i.e. total species richness for each elevation zone. This method of interpolating species presence between known elevation range limits has commonly been used to investigate species richness patterns along elevation gradients (e.g. Patterson *et al.*, 1996, 1998; Rahbek, 1997; Brühl *et al.*, 1999; Odland & Birks, 1999). Although this is a weak method compared to direct field studies, it may serve as a first approximation in a top-down approach to the analysis of the relationship between species richness and endemic richness. There is always a high degree of uncertainty in the estimates of biological variables towards the endpoints of environmental gradients compared to the centre. This has been discussed in relation to compositional gradients (Hill & Gauch, 1980), species response curves (Austin & Nicholls, 1997) and species richness gradients (Colwell & Lees, 2000; Grytnes & Vetaas, 2002). Based on the findings in Grytnes & Vetaas (2002), the present analysis focuses on the elevation gradient between 1000 and 5000 m a.s.l., whereas the elevation gradient for flowering plants extends from 50 to 6000 m a.s.l. Within this focal range of the Himalayan elevation gradient we aim: (i) to see if the maxima in gamma diversity for flowering plants and the endemic subset of these plants are coherent or not, (ii) to estimate the location of these maxima on a crude scale when estimated area is incorporated and (iii) to evaluate the predictions based on hard boundary theory and Stevens' elevational Rapoport effect.

MATERIALS AND METHODS

Location

The Himalayan elevation gradient is one of the longest bioclimatic elevation gradients in the world. Within only 150 km one moves from a tropical zone to a zone of permanent frost (Fig. 1). There is a tropical/subtropical climate on the southern plains in Nepal (Terai) to *c.* 1000 m a.s.l., characterized by agricultural land and natural forest of *Shorea robusta*, *Acacia catechu* and *Dhalbergia sisso*. In the warm-temperate zone (1000–2000 m a.s.l.) *Schima–Castanopsis* forest and *Pinus roxburghii* are found between the agricultural fields. Various oak and laurel forests dominate the cold-temperate zone up to 3000 m a.s.l. The subalpine zone to 4000 m a.s.l. has *Abies spectabilis*, *Pinus wallichinana* and *Betula utilis* forests and shrubs of *Rhododendron* spp. and *Juniperus* spp. In the alpine zone above 4000 m there are also shrubs, but grassland is more common. In the high alpine zone the vegetation is more fragmented and includes common alpine genera such as *Saxifraga*, *Gentiana* and *Androsace*.

Data source

We used data on elevation ranges in the *Enumeration of flowering plants in Nepal* (Hara *et al.*, 1978; Hara & Williams, 1979; Hara *et al.*, 1982) to describe the pattern of species richness along the elevation gradient. The same source has information on the geographical range for each species, which was used to define two types of endemic species, i.e. endemic to Nepal and endemic to the Himalayas. The latter
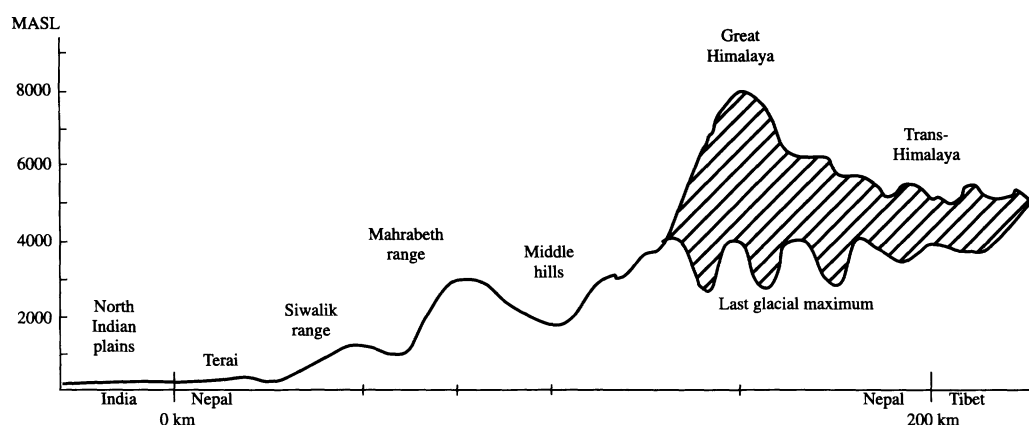
Fig. 1 A transect through Nepal from south-west to north-east, indicating the three main mountain ranges, and the location of the adjacent North Indian plains and the Tibetan plateau.

group of species includes species in the first group (Nepal) plus species found along the Himalayan range from Jammu to Kashmir in the west to the north-eastern part of India, and also includes the Trans-Himalayan zone in the border area between Nepal and Tibet. The elevation limits are given for 4928 taxa and are based on approximately 100 000 herbarium specimens in addition to the field experience of the authors of *Enumeration of flowering plants in Nepal* (Hara *et al.*, 1978). We divided the elevation gradient between 1000 and 5000 m a.s.l. into 40 100-m vertical intervals (see below). A species was defined as present at every 100-m interval between the upper and lower elevation limits. This is an estimate of gamma diversity (originally introduced by R.H. Whittaker, e.g. Whittaker (1972)), defined as total richness of an entire elevation zone (*sensu* Lomolino, 2001). For simplicity we use the terms species richness and endemic richness, because diversity is often used for indices combining richness and evenness.

Area and bias

Area and topographic heterogeneity

It is a well-established fact that species number increases as a function of area (e.g. Gleason, 1922; Rahbek, 1997; Rosenzweig, 1997). The different 100-m intervals used in our analyses do not represent equal areas because of the topography of Nepal. An exact estimate of the area for each 100-m interval is not available, but a crude estimate of the area was made by the International Centre for Integrated Mountain Development (ICIMOD Kathmandu), based on a digitized map of Nepal with 500 m contours. These data are used here to correlate endemic and species richness with log-area. However, the two-dimensional area is less accurate for elevation zones with high topographic heterogeneity. Figure 1 illustrates that the Himalayas in Nepal consist of three ranges running

south-east to north-west in Nepal: the Siwalik range (maximum 1000–15000 m a.s.l.), Marabeth range (2700–3000 m a.s.l.), and great Himalayas (5000–8000 m a.s.l.) (Hagen, 1969). Thus topographic heterogeneity varies along the elevation gradient. The number of isolated elevation-isolines that must be abstracted to find the area at a certain elevation zone indicates the topographic variation. We used this information to estimate an adjusted-area, which incorporates this inaccuracy. The adjusted-area estimates were calculated as follows: in each 500-m elevation zone we increased the two dimensional area by $\times$%, where $\times$ equals the number of isolated elevation-isolines (above one) found in each 500-m elevation zone (e.g. if $\times$ = 100 the adjusted-area is twice as large as the area unadjusted). Species richness and endemic richness were then correlated with log-adjusted-area. We used a GAM smoother (Hastie & Tibshirani, 1990) with four degrees of freedom to explore the pattern of these data between 1000 and 5000 m a.s.l.

Interpolation method, sampling intensity and auto-correlation

Although the method of interpolating species presence between elevation range limits has commonly been used to investigate species richness patterns along elevation gradients (e.g. Stevens, 1992; Patterson *et al.*, 1996, 1998; Rahbek, 1997; Brühl *et al.*, 1999; Nathan & Werner, 1999; Odland & Birks, 1999), the possible artefacts due to interpolation have not been discussed previously. Grytnes & Vetaas (2002) demonstrated in a simulation study on the same elevation gradient that the interpolation method underestimates species number at the gradient extremes (approximately 1000 m from the extremes in the present gradient). Thus this study focuses on the potential coherence between species richness and endemic richness between 1000 m and 5000 m a.s.l. In addition we checked the species richness and endemic

richness patterns for species that occur in only one or two adjacent 100-m intervals. These will be based only on observation, and not interpolation.

A focus on the range between 1000 and 5000 m a.s.l. is also justified by the fact that the lowland forest was transformed to agricultural land before the main floristic inventories in Nepal were made (Hara et al., 1978). Botanical surveys in Nepal have not sampled the lowland with the same intensity as the higher elevations, probably as a result of the Himalayan Mountains being the main attraction to botanists (Dobremez, 1976: 97). It is also reasonable to assume that the sampling intensity beyond 5000 m a.s.l. is low.

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. This positive autocorrelation will be enhanced by the interpolation method as we assume that species are present in all elevation zones between the range limits, thereby ignoring all real disjunctions in species distribution along the elevation gradient. However, an autocorrelated response variable is a problem mainly when explicit causal factors are being tested (Legendre, 1993; Lennon, 2000). In this study we focus on the potential coherence between total richness and endemic richness without using causal tests, but we test if certain patterns along the elevation range are statistically significant, when elevation is the explanatory variable. We used an F-test for all analyses since the deviances were over- or under-dispersed (Hastie & Pregibon, 1993), but these results have primarily a descriptive value and do not follow the strict assumptions of inferential statistics because of spatial auto-correlation.

Analytical methods

Simple scatter plots show the patterns of species richness and endemic richness, where the horizontal axes are defined by elevation and the vertical axes by species richness or endemic richness. This was done for (1) total species richness, (2) total richness excluding species endemic to Nepal, (3) total richness excluding species endemic to the Himalayas, (4) the number of endemic species restricted to Nepal and (5) the number of endemic species restricted to the Himalayan range. We also displayed the ratio of endemic species (4 and 5) to the total species number (1). We used general additive models (GAM: Hastie & Tibshirani, 1990) with up to three degrees of freedom to evaluate the significance of specific trends for total species richness with and without Nepal endemics: (1) a monotonic decreasing vs. a unimodal trend for the total elevation gradient, (2) if a plateau exists in the intervals 1000–2500 m a.s.l. and 3000–4000 m a.s.l. and (3) if there was a unimodal or a monotonic pattern for species with very narrow elevation ranges.

RESULTS

There are 303 species that are endemic to Nepal according to Hara et al. (1978). There are 1957 species growing in Nepal that have their distribution restricted to the Himalayan range. The plants that are endemic to Nepal have an average elevation range of 605 m, while species endemic to Himalayas have an average range of 855 m and the overall average range is 928 m (excluding endemic species). Thus, as expected, the endemic species have a smaller elevation range than the total species pool (excluding endemic species).

There is a significant monotonically increasing trend in total species richness (Fig. 2a) from 1000 m to 2500 m a.s.l. From 2500 to 4000 m a.s.l., there is a clear and gentle decrease, except for a plateau between 3000 and 4000 m a.s.l. (Table 1a). Above 4000 m there is a very steep decrease towards 5000 m a.s.l. (Fig. 2a). Thus the total gradient has a humped pattern in species richness if all species are included. When species endemic to Nepal are excluded from the total (Table 1b), the trend in the interval from 1000 m to 2500 m is not statistically significant and there is a clear and gentle decrease from 3000 to 4000 m (Fig. 2b).

The species endemic to Nepal have a clear, unimodal response along the elevation gradient (Fig. 2d). It increases monotonically from 1000 to 3500 m a.s.l. Between 3500 and 4500 m a.s.l., there is a peak in endemic species and beyond 4500 m it decreases steeply towards 5000 m a.s.l. The ratio of species endemic to Nepal increases more or less monotonically from low to high elevations, but above 4500 m there is a drop before it increases again (Fig. 2f). The species endemic to the Himalayas increase monotonically up to around 4000 m a.s.l., and beyond 4000 m there is a steep decrease towards 5000 m (Fig. 2e). The proportion of Himalayan endemic species increases very steadily from low to high elevations (Fig. 2g). There is no overlap in the maxima of total richness and endemic richness, but the latter coincides with a dramatic drop in species richness from 4000 m and above.

Figure 3 illustrates on a crude scale (500-m interval) how area and topographic heterogeneity vary along the elevation gradient and their potential effect on diversity patterns. The peak in endemism is not affected by area (Fig. 3), but total species richness has a peak at higher elevations when log-area is incorporated. This assumes a strong positive linear species–area relationship. There is no significant positive correlation between log-area and total species richness ($r = 0.49$; $n = 8$) or when Nepal endemics are excluded ($r = 0.54$). When area is adjusted for topographic heterogeneity the correlations are significant for total richness ($r = 0.69$, $n = 8$) and when Nepal endemics are excluded ($r = 0.73$). Negative correlations are found between area and the number of endemic species (Nepal: $r = -0.83$; Himalayas $r = -0.76$; $n = 8$). The correlations are also negative when area is adjusted (Nepal: $r = -0.79$; Himalayas $r = -0.62$). The latter

© 2002 Blackwell Science Ltd, Global Ecology & Biogeography, 11, 291–301
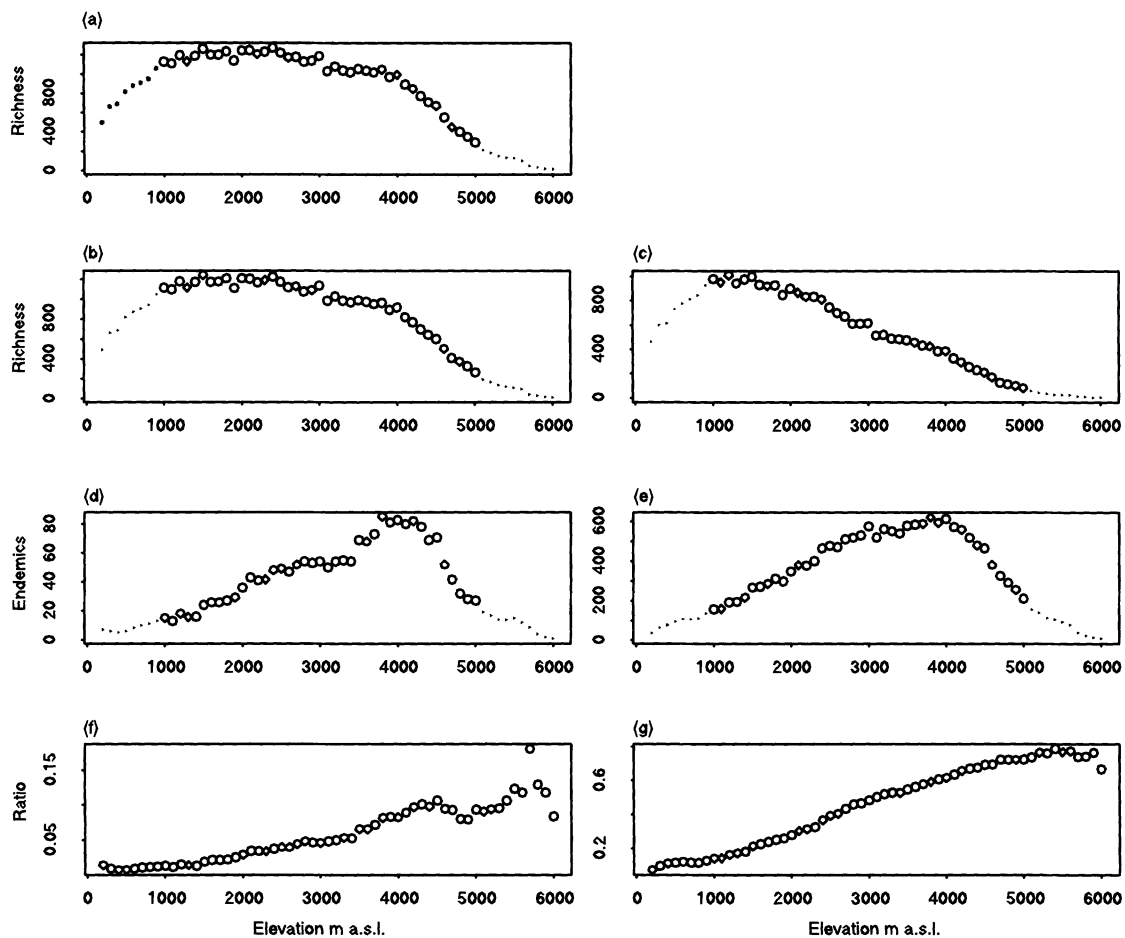
Fig. 2 Variation in diversity along the elevation gradient in Nepal. Species richness: (a) total richness, (b) excluding species endemic to Nepal, (c) excluding species endemic to the Himalayas. Endemic richness: (d) Nepal endemics, (e) Himalaya endemics. Ratio between endemic species and total richness: (f) Nepal and (g) the Himalayas. Data points outside the focal range between 1000 and 5000 m a.s.l. are uncertain and show small dots.

is not statistically significant as the correlation coefficient must exceed 0.67 when the number of samples is eight. If we use log-species-richness instead of species richness there are no significant positive correlations.

Taxa with a narrow range (100–200 m) have the following pattern: total species richness decreases from the lowlands to the highlands, and species endemic to Nepal and Himalayas both have peaks around 4000 m a.s.l. (Fig. 4).

DISCUSSION

There is no overlap between the interval of maximum endemic species (3800–4200 m a.s.l.) and maximum species richness (1500–2500 m a.s.l.). The exact location of maximum species density (i.e. number of specie per area) is uncertain and its accuracy depends on ecologically sound estimates of area (cf. below). The decrease in species richness from c.

2500 m a.s.l. and upwards confirms the rule of reduced species number with higher elevation (Colwell & Hurtt, 1994 and references therein). This is due probably to ecophysiological constraints, such as reduced growing season, low temperatures, low energy (Körner, 1999; Brown, 2001) and mountain barriers against the closest species pool at the Tibetan plateau (Fig. 1), i.e. the hard boundary (Colwell & Lees, 2000; Grytnes & Vetaas, 2002).

Different maxima of endemic and species richness was conjectured from the hard boundary model, but they reject the hypothesis tentatively deduced from Rapoport's elevational rule (Stevens, 1992). Here endemic species should increase towards the lowlands since by definition, they have a narrow geographical range. However, the species with a very narrow elevation range decrease from low to high elevation (Fig. 4), which agrees with Stevens' theory (1992). Despite this pattern, the proportion of endemic species and their

Table 1 Regression statistics for general additive models for specific elevation intervals. (a) Total species richness is the response variable and smooth function of metres above sea level (m-asl) is the explanatory variable. (b) The species endemic to Nepal are excluded from the total number of species

Interval m-a.s.l.	T-dev	T-d.f.	Res-dev	Res-d.f.	% Dev-expl	P (F)
(a)						
1000–5000	3421.2	39	1371.8	37.9	58.7	$P < 0.001$
			411.5	36.9	87.7	$P < 0.001$
			198.0	35.9	93.7	$P < 0.001$
1000–2500	26.47	14	16.9	13.0	31.2	$P < 0.001$
			15.3	11.9		$P = 0.20$
3000–4000	7.86	9	3.7	5.9		$P = 0.19$
(b)						
1000–5000	3674.6	39	1267.7	38.0	67.4	$P < 0.001$
			355.9	36.9	89.8	$P < 0.001$
			166.5	36.0	95.1	$P < 0.001$
1000–2500	19.8	14	16.4	13.0		$P = 0.125$
			14.6	11.9		$P = 0.161$
3000–4000	13.6	9	4.2	8.0	65.3	$P < 0.003$
			3.5	7.0		$P = 0.272$

Interval m-a.s.l. = interval analysed in m a.s.l.; T-dev = total deviance; T-d.f. = total degrees of freedom, Res-dev = residual deviance; Res-d.f. = residual degrees of freedom; % Dev-expl = percentage deviance explained, P (F) = probability of F-test.

absolute numbers decrease towards the lowlands (Fig. 2d–g). There are obvious reasons for a reduced chance of isolation in the Nepalese lowland as the environment becomes more similar to that of the large northern Indian plains surrounding it, and the physical environment has relatively little topographic variation (Fig. 1). The vegetation is, and has been, influenced strongly by human activity, and endemics may have been differentially extirpated compared with large-range non-endemics. As a result, endemics may have a peak at higher elevations than total species richness.

The peak in endemic richness is confirmed by the fact that endemic species with narrow elevation ranges (100–200 m) also have a peak around 4000 m (Fig. 4b,c). Thus the location of maximum endemic richness is not an artefact due to the interpolation method. The same peak is also found when the number of endemics is divided by log-area (or adjusted-area) in each 500 m zone (Fig. 3g–i), whereas the total species density appears at the mid-elevation, concordant with the hard boundary theory (Fig. 3e–f) (Colwell & Lees, 2000; Grytnes & Vetaas, 2002). Thus, the peak in endemic richness is at a higher elevation than the peak in total species richness, but the exact peak in total species density is dependent on the area estimates. To account for area by simply dividing the number of species in each elevation zone by the area in this zone assumes a strong positive log-linear relationship between species richness and area. This was not confirmed, but for total species richness there is a significant relationship when area is adjusted for topographic heterogeneity. However, the data points are very few, and subsequently the

statistical power is low and the probability of Type II error is high. If one accepts that the species–area relationships is an ecological truism, the crude analyses here indicate that the two-dimensional representation of area is not a good estimate of the actual available surface, which is better estimated as volumes (Rahbek, 1997) or fractal dimensions (Palmer, 1992). This illustrates that one has to be very careful in using the two-dimensional area in large and steep mountain ranges.

High elevation pattern

Whereas the proportion of endemic species increases with elevation, the absolute number decreases above 4000 m. The proportional increase is due mainly to a sharp decrease in overall species richness. This is different from data in eastern Europe, which indicate maximum proportions in the subalpine zone (Major, 1988), where the absolute number has a maximum in the Himalayas.

The most striking feature in Fig. 2 is that the maximum numbers of endemic species (both types) coincide with a sudden drop in species richness that starts at 4000 m a.s.l. and continues to 5000 m a.s.l. This pattern may relate to factors such as (i) timberline and (ii) glaciation limits that can generate different degrees of dispersal limits and will appear as environmental hard boundaries as indicated by Colwell & Lees (2000).

(i) The timberline in Nepal is found around 4000 m a.s.l. The upper elevation limits for *Abies spectabilis*, *Pinus wallichiana* and *Betula utilis* are 4000–4300 m a.s.l., respectively.
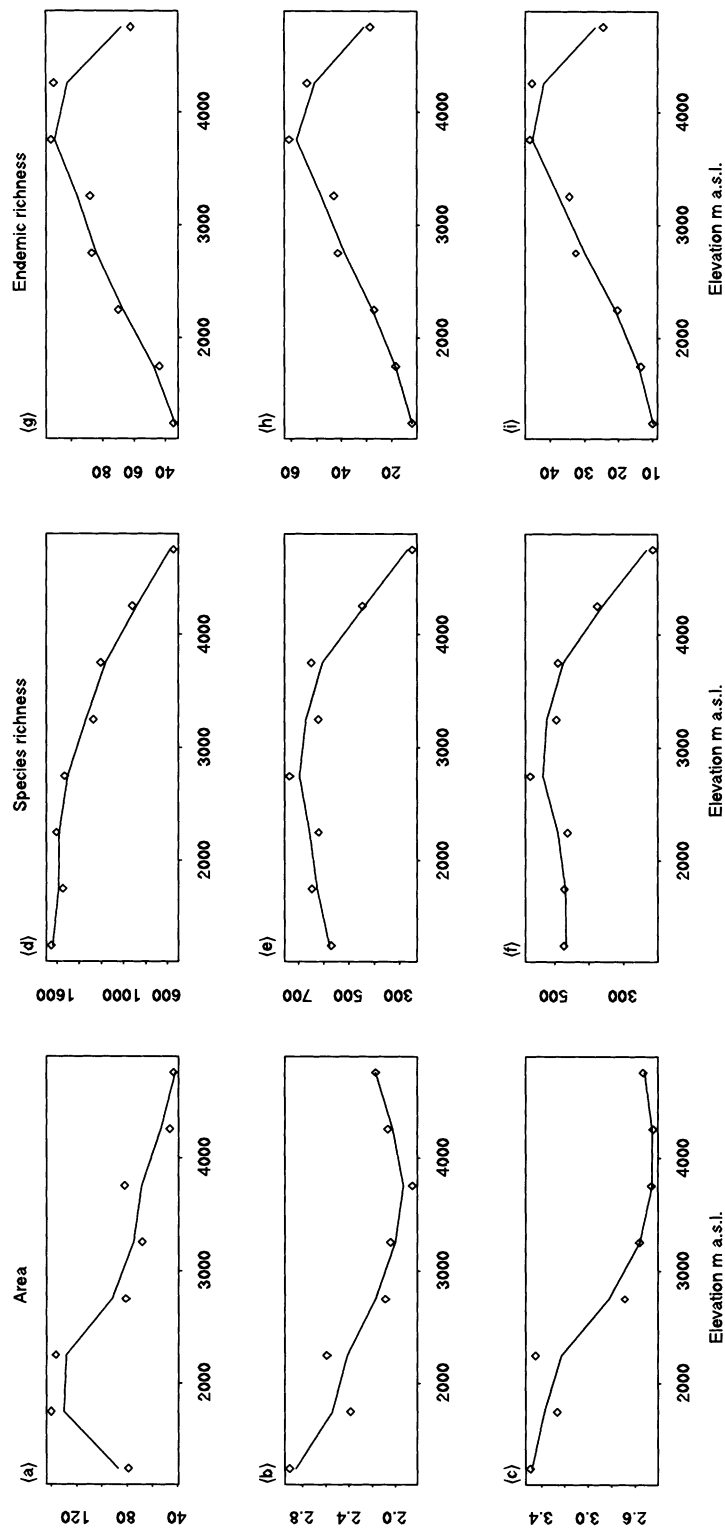
Fig. 3 Scatter plots based on data from elevation intervals of 500-m. Data on area (first column), total richness excluding Nepal endemics (middle column), and species endemic to Nepal, are plotted against elevation (1000–5000 m a.s.l.). (a) Number of isolated elevation-isolines, (b) log-area (1000 km²), (c) log-area-adjusted, (d) species richness, (e) species richness/log-area, (f) species richness/log-area-adjusted, (g) endemic richness, (h) endemic richness/log-area and (i) endemic richness/log-area-adjusted. Area was adjusted for topographic heterogeneity by increasing the two-dimensional area 1% for each isolated elevation-isoline in the 500-m elevation zones (see text). The regression lines were fitted by general additive modelling with four degrees of freedom.
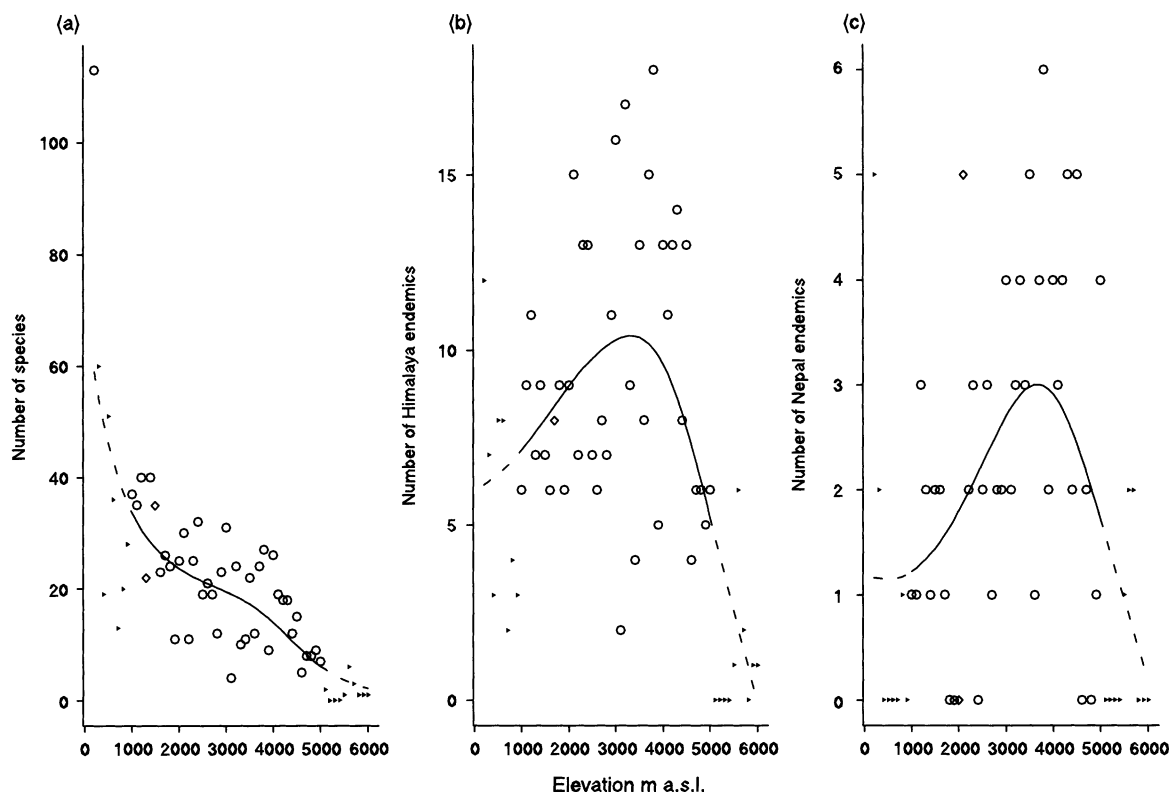
Fig. 4 Number of species with a very narrow elevation range (100–200 m) plotted against the elevation gradient in Nepal: (a) all species (n = 1078), (b) species endemic to the Himalayas (n = 399) and (c) species endemic to Nepal (n = 105). The regression lines fitted by general additive modelling are statistically significant for all cases (P < 0.001). Data points outside the focal range between 1000 and 5000 m a.s.l. are uncertain and have small dots (broken line).

These trees form subalpine forests in relatively moist habitats close to the limit of tree growth (Polunin & Stainton, 1986). Open grassland and shrubby vegetation of juniper and rhododendron are present both below and above the timberline, but above the timberline the shrubs are dominant. Thus the relatively moist and shady microenvironment found in subalpine forests is absent. Since the subalpine forests often have a limited extent on northerly exposed moist slopes where they are surrounded by more xeric shrubby vegetation, they may act as refugia for certain species. However, only *c*. 15 of the 114 endemic species that occur between 3500 and 4500 m a.s.l. are restricted to subalpine forests (cf. Polunin & Stainton, 1986; Shrestha & Joshi, 1996). Thus the forest limit does not explain the peak in endemic species. However, the reduction in habitat diversity above the forest limit may relate to the sharp reduction in species richness above 4000 m a.s.l. There is less variation from west to east in vegetation above the timberline (4000–4300 m) compared with the intermediate elevation zones (Shrestha & Joshi, 1996).

(ii) The literature indicates large variation in the maximum lower extent of glaciers during maximum glaciation (von Wissmann, 1959; Williams, 1983; Duncan *et al.*, 1998; and references therein). Although the maximum extent varies along the Himalayan range, the equilibrium line altitude (ELA) probably descended to about 4000 m a.s.l. (Duncan *et al.*, 1998), and glacier arms have deposited glacial material at 3200 and 2300 m a.s.l. in certain valleys (Iwata *et al.*, 1982; Shiraiwa & Watanbe, 1991).

Colwell & Lees (2000) state that it is important to assess the effectiveness of biogeographical boundaries in relation to the temporal scale at which they are operative, and to remove the effects of geometry (i.e. a hard boundary) and then to look afresh at the environmental and historical influences on richness gradients. The variation in glacial extent during the Quatenary may have determined the degree of resistance to dispersal, and can be viewed as a dynamic hard boundary. However, it is not easy to factor out the effect of hard boundaries when the boundary is controlled by climate change during the glacial history at various temporal scales such as the Pleistocene, Holocene, and the 'Little Ice Age'. This dynamic hard boundary controlled by climate may explain the sudden drop in species richness above 4000 m, and may

also explain the elevated number of endemic species (both types) around 4000 m a.s.l. Endemic species between 3500 and 4500 m a.s.l. are mostly found in open moist habitats (Polunin & Stainton, 1986; Shrestha & Joshi, 1996). Only 12 endemic species are associated with vegetation of the dry inner valleys, which form a part of the Trans-Himalayan region that extends onto the Tibetan plateau (Fig. 1). The habitat described for endemic species (Polunin & Stainton, 1986; Shrestha & Joshi, 1996) is typical of landscapes generated by glacier activity, such as sandy river banks, screes, moraines and slopes with boulders. It is therefore not unlikely that many endemic species have originated in a landscape fragmented by glacial advances and retreats. The glacier arms that covered the valley bottoms below the ELA must have acted as dispersal barriers, which enhanced the physical barriers created by the mountains (see, e.g. Willis & Whittaker, 2000), i.e. providing a mechanism for increased isolation. Stebbins (1984) argues that large-scale glacier dynamics may facilitate hybridization between previously isolated populations, followed by either polyploidy or introregression at the diploid level, which may generate new species adapted to the conditions following ice retreat. Thus one should expect a high polyploidy ratio among these neo-endemic species. Several of the genera that represent endemic 'swarms' in the Himalayas, such as *Primula*, *Aconitum* and *Saxifraga* (Nayar, 1996), have many polyploid species both in the Himalayas and elsewhere (Kadota, 1987; Sakya & Joshi, 1990; Solitis *et al.*, 1996). It has been proposed that polyploids have greater resistance to the severe conditions found at high elevations (or latitudes) and they often have a breeding system (e.g. apomixis) that is well-adapted to a short growing season (Grant, 1971; Stebbins, 1984). Several other studies have associated polyploidy with glaciation limits (Jay *et al.*, 1991; Gornall & Wentworth, 1993; Dufresne & Hebert, 1997), and Lumaret *et al.* (1997) suggest that survival of polyploid taxa may be favoured by conditions with long-term habitat fragmentation.

Based on these ideas, one may hypothesize that a high level of endemic species may be favoured by high species richness close to an area where isolation is combined with low rates of competitive displacement (Huston, 1994), such as on glacially modified landscapes. Mountain chains where glaciers enhance the probability of isolation may facilitate survival of new species created by polyploidy and hybridization. At a large biogeographical scale, species richness and endemic richness actually coincide with each other, as shown here with a high diversity in Himalayas and a high endemic fraction in the Himalayas as a whole.

ACKNOWLEDGMENTS

REFERENCES

Austin, M.P. & Nicholls, A.O. (1997) To fix or not to fix the species limits, that is the ecological question: response to Jari Oksanen. *Journal of Vegetation Science*, 8, 743–748.

Brown, J. (2001) Mammals on mountainsides: elevational patterns of diversity. *Global Ecology and Biogeography*, 10, 101–109.

Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*, 2nd edn. Sinauer Associates. Inc. Publishers, Sunderland, MA.

Brühl, C.A., Mohamed, M. & Linsenmair, K.E. (1999) Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. *Journal of Tropical Ecology*, 15, 265–277.

Carlquist, S. (1974) *Island biology*. Columbia University Press, New York.

Colwell, R.K. & Hurtt, G.C. (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist*, 144, 570–595.

Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, 15, 70–76.

Dobremez, J.F. (1976) *Le Népal: écologie et biogéographie*. Centre National de la Rechereche Scientifique, Paris.

Dufresne, F. & Hebert, P.D.N. (1997) Pleistocene glaciation and polyphyletic origins of polyploidy in an arctic cladoceran. *Proceedings of the Royal Society of London, Biological Sciences*, 264, 201–206.

Duncan, C.C., Klein, A.J., Masek, J.G. & Isacks, B.L. (1998) Comparison of late Pleistocene and modern glacier extent in central Nepal based on digital elevation data and satellite imagery. *Quaternary Research*, 49, 241–254.

Gentry, A.H. (1986) Endemism in tropical versus temperate plant communities. *Conservation biology: the science of scarcity and diversity* (ed. by M. Soulé), pp. 153–181. Sinauer Associates, Inc. Publishers, Sunderland, MA.

Gleason, H.A. (1922) On the relation between species and area. *Ecology*, 3, 213–225.

Gornall, R.J. & Wentworth, J.E. (1993) Variation in the chromosome-number of *Parnassia-palustris* L. in the British Isles. *New Phytologist*, 123, 383–388.

Grant, V. (1971) *Plant speciation*. Columbia University Press, New York.

Grytnes, J.A. & Vetaas, O.R. (2002) Species richness and altitude: a comparison between simulation models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *American Naturalist*, 159, 294–304.

Hagen, T. (1969) Report on the Geological survey of Nepal. *Denckschrift der Schweizerischen Naturforschenden Gesellschaft*, 86, 1–160.

Hara, H., Chater, A.O. & Williams, H.J. (1982) *An enumeration of the flowering plants of Nepal*, III. British Museum Natural History, London.

Hara, H., Stearn, W.T. & Williams, H.J. (1978) *An enumeration of the flowering plants of Nepal*, I. British Museum Natural History, London.

Hara, H. & Williams, H.J. (1979) *An Enumeration of the Flowering Plants of Nepal*, II. British Museum Natural History, London.

Hastie, T.J. & Pregibon, D. (1993) Generalized linear models. *Statistical models in S* (ed. by J.M. Chambers and T.J. Hastie), pp. 195–247. Chapman & Hall, London.

Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized additive models.* Chapman & Hall, London.

Heaney, L.R. (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, 10, 15–39.

Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis — an improved ordination technique. *Vegetatio*, 42, 597–613.

Hobohm, C. (2000) Plant species diversity and endemism on islands and archipelagos, with special reference to the Macaronesian Islands. *Flora*, 195, 9–24.

Huston, M.A. (1994) *Biological diversity — the coexistence of species on changing landscapes.* Cambridge University Press, Cambridge.

Iwata, S., Yamanaka, H. & Yoshida, M. (1982) Glacial landforms and river terraces in the Thakhola region, central Nepal. *Journal of the Nepal Geological Society*, 2, 81–94.

Jay, M., Reynaud, J., Blaise, S. & Cartier, D. (1991) Evolution and differentiation of populations of *Lotus corniculatus Lotus-alpinus* populations from French south-western Alps. 3. Conclusions. *Evolutionary Trends in Plants*, 5, 157–160.

Kadota, J. (1987) *A revision of* Aconitum *sub genus* Aconitum *(Ranunculaceae) of eastern Asia.* Sanwa Shoyaku Co., Japan.

Körner, C. (1999) *Alpine plant life.* Springer Verlag, Berlin.

Körner, C. (2000) Why are there global gradients in species richness? Mountains may hold the answer. *Trends in Ecology and Evolution*, 15, 513–514.

Kunkel, G. (1992) *Die Kanarischen Inseln und ihre Pflanzenwelt*, 3rd edn. Fischer, Stuttgart.

Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74, 1659–1673.

Lennon, J.J. (2000) Red-shifts and red herrings in geographical ecology. *Ecography*, 23, 101–113.

Lieberman, D.M., Lieberman, R. & Peralta & Hartshorn, G.S. (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, 84, 137–152.

Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, 10, 3–13.

Lumaret, R., Guillerm, J.L., Maillet, J. & Verlaque, R. (1997) Plant species diversity and polyploidy in islands of natural vegetation isolated in extensive cultivated lands. *Biodiversity and Conservation*, 6, 591–613.

Major, J. (1988) Endemism: a botanical perspective. *Analytical biogeography* (ed. by A.A. Myers and P.S. Giller), pp. 117–146. Chapman & Hall, London.

Md. Nor, S. (2001) Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography*, 10, 41–62.

Nathan, R. & Werner, Y.L. (1999) Reptiles and breeding birds on Mt. Hermon: patterns of altitudinal distribution and species richness. *Israel Journal of Zoology*, 45, 1–33.

Nayar, M.P. (1996) *Hot spots of endemic plants of India, Nepal, and Bhutan.* Tropical Botanic Garden and Research Institute, Palode, Thiruvananthapuram, India.

Odland, A. & Birks. H.J.B. (1999) The altitudinal gradient of vascular plant species richness in Aurland, western Norway. *Ecography*, 22, 548–566.

Palmer, M.W. (1992) The coexistence of species in fractal landscapes. *American Naturalist*, 139, 375–397.

Patterson, B.D., Pacheco, V. & Solari, S. (1996) Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology*, 240, 637–658.

Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W. & Pacheco, V. (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography*, 25, 593–607.

Polunin, O. & Stainton, A. (1986) *Flowers of the Himalayas.* Oxford University Press, Dehli.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, 18, 200–205.

Rahbek, C. (1997) The relationship among area, elevation and regional species richness in neotropical birds. *American Naturalist*, 149, 875–902.

Rapoport, E.H. (1982) *Areography: geographical strategies of species* (English edition translated by Drausal, B.). Pergamon Press, New York.

Raven, P.H. & Axelrod, D. (1978) The origin and relationship of the California flora. University. *California Publication in Botany*, 72, 1–135.

Rickart, E.A. (2001) Elevational diversity gradients, biogeography, and the structure of montane mammal communities in the inter-mountain region of North America. *Global Ecology and Biogeography*, 10, 77–100.

Rosenzweig, M.L. (1997) *Species diversity in space and time*, 2nd edn. Cambridge University Press, Cambridge.

Sakya, S.R. & Joshi, K.K. (1990) Karyomorphological studies in some *Primula* species of Nepal Himalaya. *Cytologia*, 55, 571–579.

Sánchez-Cordero, V. (2001) Small mammal diversity along elevational gradients in Oaxaca, Mexico. *Global Ecology and Biogeography*, 10, 63–76.

Shiraiwa, T. & Watanbe, T. (1991) Late Quatenary glacial fluctuations in the Langtang valley, Nepal Himalaya, reconstructed by relative dating methods. *Arctic and Alpine Research*, 23, 404–416.

Shmida, A. & Wilson, M.W. (1985) Biological determinants of species diversity. *Journal of Biogeography*, 12, 1–20.

Shrestha, T.B. & Joshi, R.M. (1996) *Rare, endemic, and endangered plants in Nepal.* WWF Nepal Program, Kathmandu, Nepal.

Solitis, D.E., Kuzoff, R.K., Conti, E., Gornall, R. & Ferguson, I.K. (1996) MatK and rbcL gene sequence data indicate that *Saxifraga* (Saxifragaceae) is polyphyletic. *American Journal of Botany*, 83, 371–382.

Stebbins, G.L. (1984) Polyploidy and distribution of the arctic-alpine flora: new evidence and new approaches. *Botanica Helvetica*, 94, 1–13.

Stevens, G.C. (1992) The elevation gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist*, 140, 893–911.

Tobler, W.R. (1969) Geographical filters and their inverse. *Geographical Analysis*, 1, 234–253.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279–338.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, 21, 213–251.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453–470.

Williams, V.S. (1983) Present and former equilibrium-line altitude near Mount Everest, Nepal and Tibet. *Arctic and Alpine Research*, 15, 201–211.

Williamson, M.H. (1981) *Island populations*. Oxford University Press, Oxford.

Willis, K.J. & Whittaker, R.J. (2000) The refugial debate. *Science*, 287, 1406–1407.

von Wissmann, H., (1959) Die heutige Vergletscherung und Schneegrenze in Hochasien mit inweisen auf die Vergletscherung der lezten Eisziet. Akademie der Wissenschaften und der Literatur in Mainz. *Abhandlungen der Mathematisch-Aturwissenschaftlichen Klasse*, 14, 1101–1431.

BIOSKETCHES

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).

John-Arvid Grytnes is a doctoral student at the Department of Botany, UoB. His interests are patterns in plant diversity at different scales, such as the relationship between richness and productivity in alpine vegetation, and biogeographical and altitudinal richness gradients in Fennoscandia and the Himalayas.