



A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya

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ABSTRACT

Aim To explore species richness patterns in liverworts and mosses along a central Himalayan altitudinal gradient in Nepal (100–5500 m a.s.l.) and to compare these patterns with patterns observed for ferns and flowering plants. We also evaluate the potential importance of Rapoport's elevational rule in explaining the observed richness patterns for liverworts and mosses.

Location Nepal, Central Himalaya.

Methods We used published data on the altitudinal ranges of over 840 Nepalese mosses and liverworts to interpolate presence between maximum and minimum recorded elevations, thereby giving estimates of species richness for 100-m altitudinal bands. These were compared with previously published patterns for ferns and flowering plants, derived in the same way. Rapoport's elevational rule was assessed by correlation analyses and the statistical significance of the observed correlations was evaluated by Monte Carlo simulations.

Results There are strong correlations between richness of the four groups of plants. A humped, unimodal relationship between species richness and altitude was observed for both liverworts and mosses, with maximum richness at 2800 m and 2500 m, respectively. These peaks contrast with the richness peak of ferns at 1900 m and of vascular plants, which have a plateau in species richness between 1500 and 2500 m. Endemic liverworts have their maximum richness at 3300 m, whereas non-endemic liverworts show their maximum richness at 2700 m. The proportion of endemic species is highest at about 4250 m. There is no support from Nepalese mosses for Rapoport's elevational rule. Despite a high correlation between altitude and elevational range for Nepalese liverworts, results from null simulation models suggest that no clear conclusions can be made about whether liverworts support Rapoport's elevational rule.

Main conclusions Different demands for climatic variables such as available energy and water may be the main reason for the differences between the observed patterns for the four plant groups. The mid-domain effect may explain part of the observed pattern in moss and liverwort richness but it probably only works as a modifier of the main underlying relationship between climate and species richness.

Keywords

Altitudinal gradient, bryophytes, elevational gradient, endemism, Himalaya, liverworts, mid-domain effect, mosses, Rapoport's elevational rule, species richness.

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INTRODUCTION

The Himalaya contain the highest mountains in the world and a very wide range of ecoclimate zones (Dobremez, 1976). These mountains are therefore an excellent system for evaluating ecological and biogeographical patterns and theories of species richness (Körner, 2000). Many studies have investigated patterns of plant species richness along altitudinal gradients (e.g. Ohlemüller & Wilson, 2000; Gómez *et al.*, 2003; Grytnes, 2003; Oommen & Shanker, 2005; Kluge & Kessler, 2006). In many cases, a mid-altitude peak in species richness has been found (Rahbek, 2005). However, a linear decrease of richness with altitude has also been found in some studies (e.g. Stevens, 1992; Rey Benayas, 1995; Brown & Lomolino, 1998; Körner, 2002). Factors causing variation in species richness may differ between different organisms, resulting in different patterns (Kessler, 2000; Bhattarai & Vetaas, 2003; Grytnes *et al.*, 2006). Comparing altitudinal richness patterns between different organisms along the same gradient may therefore provide clues to what determines species richness patterns at broad scales (Lomolino, 2001). In Nepal, species richness patterns along altitudinal gradients have been analysed for vascular plant species and fern species. A humped relationship was found for both vascular plants and ferns (Vetaas & Grytnes, 2002; Bhattarai & Vetaas, 2003; Bhattarai *et al.*, 2004). In this study we focus on altitudinal patterns in liverwort and moss species richness in the same area and compare the observed patterns in species richness with the richness patterns for vascular plants and ferns.

Endemic species are of a particular interest in conservation and management and in biogeography because patterns in range-restricted species may reveal insights into processes of speciation. Vetaas & Grytnes (2002) studied the richness of endemic vascular plants in relation to altitude in Nepal. They found an elevated number of endemic vascular plant species between 3800 and 4200 m, while the fraction of endemics increased linearly from the lowlands to the highest altitudes. In this study we compare these observations with the altitudinal patterns of Nepalese endemic liverworts. Mosses have too few endemics in Nepal for such an analysis.

Climate, productivity and other energy-related variables are commonly proposed to explain species richness patterns along altitudinal gradients (Rahbek, 1997). Other hypotheses include 'Rapoport's rule' and the 'mid-domain effect'. Rapoport's elevational rule proposes that there is a positive correlation between elevation and the elevational range of species (Stevens, 1992). This is usually explained by the fact that species occurring at high elevations must be able to withstand a broad range of climatic conditions and this leads to a wide elevational range. This will, in turn, lead to more species because of a spillover effect around the range edges called a rescue effect (Stevens, 1992). Colwell & Hurtt (1994) proposed the mid-domain effect to explain mid-elevation peaks in species richness. They suggest that mid-elevation peaks in species richness arise because of the increasing overlap of species ranges towards the centre of the domain, as the extent of the

elevational ranges of species is bounded by the highest and lowest elevations, so-called hard boundaries. Contrary to Rapoport's rule, the hard-boundary hypothesis predicts that species ranges at higher elevations are narrow (Bhattarai & Vetaas, 2006). In the present study these two hypotheses are discussed in addition to climate as explanatory factors for the observed altitudinal patterns of bryophyte richness.

In summary, we have the following aims: (1) to describe the richness pattern of liverworts and mosses along the altitudinal gradient in Nepal; (2) to compare the altitudinal patterns of species richness of liverworts and mosses with the patterns found for vascular plants and ferns in the same area; (3) to compare the altitudinal patterns in richness of endemic liverworts with richness patterns of non-endemic liverworts; and (4) to evaluate the potential importance of Rapoport's elevational rule and the mid-domain effect in explaining liverwort and moss species richness along the altitudinal gradient in Nepal.

METHODS

Location and biogeography of the study area

The Himalayan altitudinal gradient is the longest bioclimatic gradient in the world extending from 60 m a.s.l. to more than 8000 m a.s.l. within 150–200 km south to north; it comprises extensive tropical/subtropical, temperate, subalpine and alpine climatic zones (Bhattarai *et al.*, 2004).

Our study area is in Nepal, which covers 900 km from east to west in the Central Himalaya (80°04'–88°12' E, 26°22'–30°27' N). The Himalaya consist of three ranges running south-east to north-west in Nepal: the Siwalik range (maximum 1000–1500 m), the Mahabharat range (maximum 2700–3000 m) and the Great Himalaya (5000–8000 m) (Hagen, 1969; Manandhar, 1999; Bhattarai *et al.*, 2004).

Beug & Miehe (1999) present a cross-section of the major vegetation types in Central Nepal in relation to altitude, topography and climate. The principal factors governing the vegetation zonation are altitude and the duration of cloud cover and mist. According to their scheme, forests of the lower foothills are represented by south-eastern impoverished stands of Asian Dipterocarpaceae forest dominated by *Shorea robusta*. Bryophyte growth is generally not great in these tropical forests. The vegetation above 1000 m is generally dominated by lauraceous trees (e.g. *Schima wallichii*, *Castanopsis indica*, *Castanopsis tribuloides*), which form subtropical evergreen forests that vary in composition from east to west. Bryophytes are present but are not luxuriant. There is a striking change in the evergreen forests below and above 2000 m, associated with the average altitude of the lower condensation level of the cloud belt. The lower cloud-forest belt (2000–2500 m) is dominated by *Pinus wallichiana*–*Quercus lanata* (2000–2500 m), *Lithocarpus elegans* (2000–2300 m) and *Quercus glauca* (2100–2500 m), and is characterized by abundant ferns, epiphytic orchids and evergreen ferns, and large foliose lichens (e.g. *Lobaria* spp.). The middle

cloud-forest belt (2500–3000 m) is dominated by *Quercus semecarpifolia*–*Tsuga dumosa* forests, and supports abundant *Calypothercium*, *Meteorium* and *Barbella* beard-mosses. In the upper cloud-forest belt (3000–4200 m) *Abies spectabilis*–*Betula utilis* forests are found, along with abundant tufts and mats of epiphytic liverworts (e.g. *Herbertus* spp., *Plagiochila* spp.). Bryophytes, both mosses and liverworts, dominate the ground layer and form extensive carpets over boulders and tree bases. Epiphytic beard-lichens (*Usnea* spp.) can be locally abundant, especially in openings in the upper cloud-forest. Large leafy liverworts (e.g. Schill & Long, 2003; Long, 2005) can also occur frequently in the subalpine *Rhododendron*–*Potentilla*–*Kobresia*–*Juniperus* communities, especially on steep north- or east-facing slopes up to an altitude of about 4800 m. Above that, up to 5200 m, the vegetation gradually becomes open and the cover and number of species of mosses and lichens often exceed the cover and richness of flowering plants (Beug & Miehe, 1999).

Data sources

For quantifying the richness patterns of mosses and liverworts in Nepal we used the data on elevational ranges published in *Mosses of Nepal* (Kattel & Adhikari, 1992) and *Liverworts of Nepal* (Kattel, 2002). The maximum and minimum altitudes known for each species are given and endemic species are also noted. Elevational limits are given for 368 liverwort and 480 moss taxa, from which in a few cases varieties or subspecies are considered as separate taxa. In this study we use the term 'species richness' for the number of taxa. The exact number of endemic mosses and liverworts growing in Nepal is not known. Chaudhary (1998) reported about 30 endemic bryophyte species in Nepal, of which only four were mosses. Kattel (2002) lists a slightly higher number of endemic bryophytes, with 33 endemic liverwort species and three mosses. Knowledge about bryophytes in Nepal is continually increasing. Species new to Nepal are being regularly reported (e.g. Zhu & Long, 2003; Long, 2005, 2006; Wilbraham & Long, 2005) and previously undescribed species are also being found in Nepal (e.g. Ochra, 1989; Furuki & Long, 1994; Long, 1999; Grolle *et al.*, 2003). Taxonomic revisions (Schill & Long, 2003; Long *et al.*, 2006) and the resolution of synonyms and erroneous records (e.g. Long, 1995) are also improving knowledge about the composition of Nepal's moss and liverwort floras. At present there are no published checklists and altitudinal distributional data that update Kattel & Adhikari (1992) and Kattel (2002). Given the current state of knowledge about Nepalese bryophytes, these two monographs (Kattel & Adhikari, 1992; Kattel, 2002) are considered adequate for this broad-scale study of species richness patterns in relation to altitude and for comparison with richness patterns in other plant groups (D.G. Long, personal communication). Data for fern and vascular plant species richness were obtained from Bhattarai *et al.* (2004) and Vetaas & Grytnes (2002), respectively.

Data analysis

The elevational gradient was divided between 100 and 5500 m for liverworts and between 100 and 5000 m for mosses. Between the upper and lower elevational limits, species were counted at every 100-m interval in the same way as in Vetaas & Grytnes (2002) and Bhattarai *et al.* (2004). This gives an estimate of gamma diversity, defined as the total richness of an entire elevational zone (*sensu* Lomolino, 2001). In this study, species richness (Peet, 1974) is defined as the number of species present in each 100-m band. When estimating species richness it was assumed that species were present in all elevational zones between the range limits (interpolation). This may create an artificially humped pattern (Grytnes & Vetaas, 2002), but in this study the main aim is to compare elevational species richness patterns for different plant groups that are all treated in the same way so as to highlight similarities or differences in where maximum species richnesses are found. Any differences in the optimal altitudes for species richness for the different groups are probably not an artefact of the interpolation method used. In addition, bryophytes are rarely found at the lowermost elevations, and because interpolations will have their largest effect on the observed pattern at the lowermost and uppermost elevations, the use of interpolation will probably not have a significant impact on the resulting bryophyte richness patterns.

To describe the species richness patterns in relation to altitude, a generalized additive model (GAM) with a cubic smooth spline (Hastie & Tibshirani, 1990), as implemented in R 2.2.1 (R Development Core Team, 2004) was used. The GAM approach is especially useful for data exploration as it makes no a priori assumptions about the type of relationship being modelled. The GAM approach contrasts with the generalized linear model approach where a priori assumptions about the relationships being modelled (e.g. a symmetrical humped relationship) are required. Richness patterns for mosses, liverworts, vascular plants and ferns were regressed against altitude and plotted for comparison.

Initially, species richness data were considered to follow a Poisson distribution as is usual for variables with discrete values (McCullagh & Nelder, 1989). However, a quasi-Poisson distribution was used because of overdispersion. The proportion of endemic vs. non-endemic liverworts was assumed to follow a binomial distribution with the number of endemics as successes and the number of non-endemics as failures. For the quasi-Poisson analyses a logarithmic link was used, and for the binomial analyses a logit link was used.

Rapoport's elevational rule was evaluated by correlating mean species altitudinal ranges for all species found in each 100-m elevational interval with altitude. This has been criticized on several grounds (Colwell & Lees, 2000). In an attempt to allow for possible artefacts we compared our observed correlations with the results from Monte Carlo simulations under a null model. The null model was made by randomly choosing one of the feasible observed altitudinal ranges for each of the observed mid-points taking into account

the boundary constraints. This approach is the same as Model 3 in Colwell & Hurtt (1994). The simulation was run 9999 times and for each permutation the same correlation between mean altitudinal range and altitude was calculated. A one-sided test was performed based on these simulations because Rapoport's rule predicts a positive correlation between mean altitudinal range and altitude. An empirical *P*-value was derived from the number of simulations with a positive correlation larger than (or equal to) the observed value.

Due to difficulties in separating the effect of interpolation and undersampling from the mid-domain effect (Grytnes & Vetaas, 2002; Zapata *et al.*, 2003), no specific randomizations were performed to test for this in this study. The mid-domain effect is therefore only discussed briefly in the discussion and compared with the simulations made in Grytnes & Vetaas (2002) for vascular plants along the same gradient. Although this is not optimal, we refrain from 'guessing' how complete the biological sampling has been in this case. As a result, the assumptions and simulations made in Grytnes & Vetaas (2002) may therefore be as reliable as anything else, given the current state of knowledge of bryophyte recording in Nepal.

RESULTS

Both moss and liverwort species richness have a clear humped relationship with altitude, with a very marked maximum at middle altitudes (Figs 1 & 2). Mosses have highest richness values at around 2500 m, whereas non-endemic liverworts reach their maximum at a slightly higher altitude, at around 2700 m. Endemic liverworts show their maximum richness at even higher altitudes, at about 3300 m.

When comparing species richness of liverwort, moss, fern and vascular plant with each other (Fig. 3), all show a

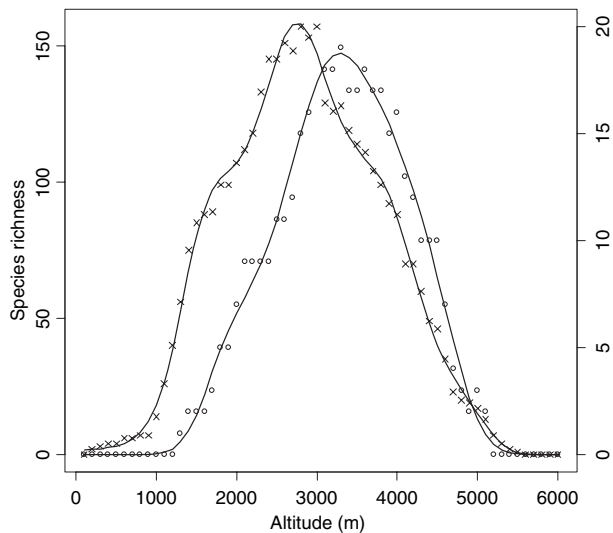


Figure 1 Non-endemic liverwort richness (x, values on the left-hand axis) and endemic liverwort richness (o, values on the right-hand axis) in relation to altitude (m) in Nepal. The fitted lines represent a GAM model with a cubic smooth spline.

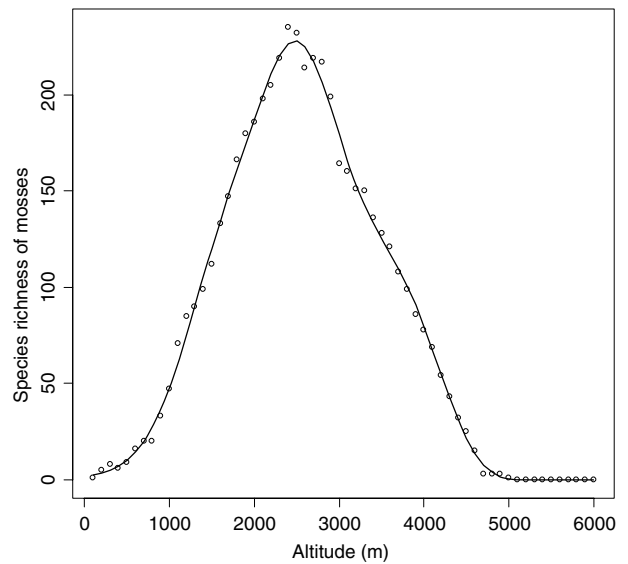


Figure 2 Moss richness in relation to altitude (m) in Nepal. The fitted line represents a GAM model with a cubic smooth spline.

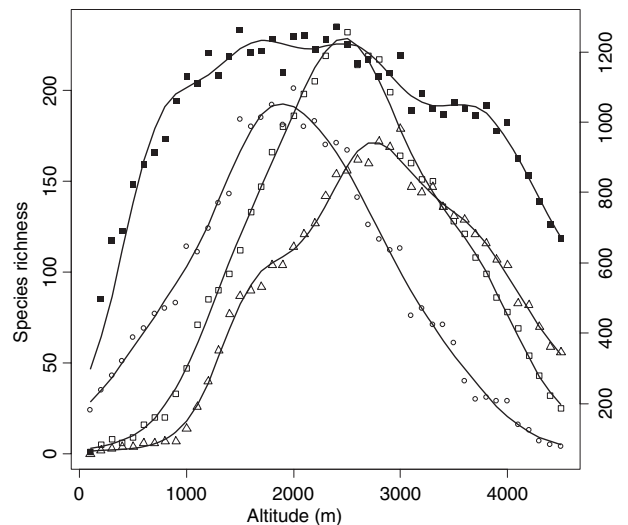


Figure 3 Fern (o), moss (square) and liverwort (triangle) richness (values on the left-hand axis) and vascular plant richness (filled square, values on the right-hand axis) in relation to altitude (m) in Nepal. The fitted lines represent a GAM model with a cubic smooth spline.

markedly humped relationship with altitude. This may be a result of underlying ecological patterns or it may, at least partly, be a result of using interpolation with data that are undersampled. We therefore focus most on the relative location of the peak in species richness when comparing the altitudinal patterns of the different plant groups. Maximum species richness for vascular plants is between 1500 and 2500 m. Fern species richness peaks at 1900 m, mosses at 2500 m and liverworts at 2800 m (if endemic and non-endemic taxa are not distinguished). There is a strong correlation between richness for the different groups (Table 1), being highest between mosses and liverworts and lowest

Table 1 Correlation between species richness along the altitudinal gradient of Nepal for different groups of plants. All correlations (Pearson's product moment correlation) are statistically significant ($P < 0.05$).

	Mosses	Liverworts	Ferns
Liverworts	0.89	–	–
Ferns	0.68	0.34	–
Vascular plants	0.74	0.59	0.74

between ferns and liverworts. The maximum elevation for mosses is achieved by *Grimmia somervillii* at 5100 m (Kattel & Adhikari, 1992). The highest elevation for liverworts is achieved by *Anastrophyllum assimile*, which reaches 5450 m (Kattel, 2002).

The proportion of endemic to non-endemic liverworts is highest around 4250 m, with a steady increase starting at around 1200 m, where the first endemic species is found (Fig. 4). The decrease in the proportion of endemics at the highest altitudes is a consequence of the lack of endemic liverworts over 5000 m.

According to our data, the altitudinal ranges of liverworts show a statistically significant increase with altitude as assessed by classical statistical tests (Fig. 5) ($r = 0.63$, $P < 0.01$) supporting Rapoport's elevational rule. In the lower altitudinal bands, the average altitudinal range is around 1500 m, whereas the species found in the highest altitudinal bands have an average altitudinal range greater than 2000 m. At first glance such results appear to support Rapoport's elevational rule. However, after running the Monte Carlo simulations, it is found that such a significant positive correlation between elevational ranges and altitude could have been obtained by chance, because the empirically derived P -value is 0.063. Such

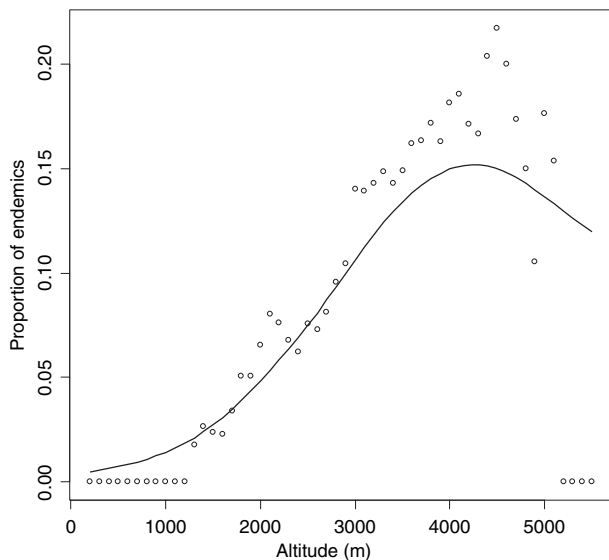


Figure 4 Proportion of endemic versus non-endemic liverwort species in relation to altitude (m) in Nepal. The fitted line represents a GAM model with a cubic smooth spline.

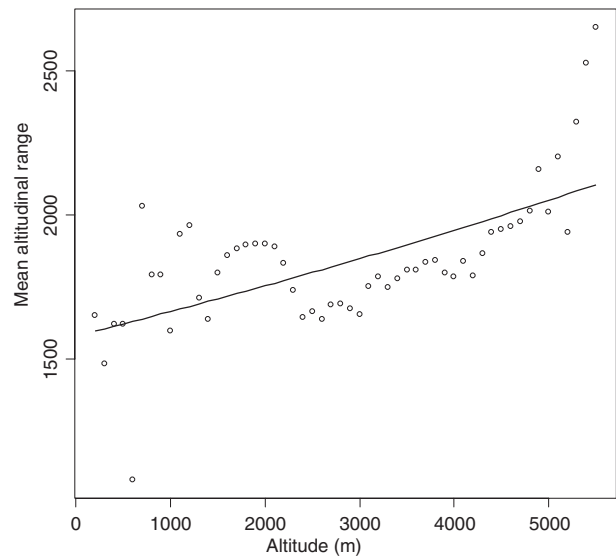


Figure 5 Liverwort altitudinal range (m) versus altitude (m) in Nepal. The fitted line represents an ordinary least square (OLS) linear regression.

a marginal P -value makes it impossible to accept or reject unambiguously the relevance of Rapoport's rule on Nepalese liverworts. Since this P -value was very close to the chosen significance level at 0.05, we performed a jack-knife (leave-one-out) analysis to investigate if the P -value was due to a single species. This was done by repeating the permutation analysis leaving out one species at the time (to reduce computing time we did 999 permutations for each species). For two of the species the P -value became lower than what is observed for all species [one of these was barely below 0.05 (0.042)]. For all the remaining species the P -values from the jack-knife analyses were higher than the P -value for all species. Mosses showed no significant positive correlation between mean altitude ranges and altitude (plot not shown, $r = -0.07$, $P > 0.1$), and the permutations confirmed this with an empirical P -value of 0.616. Thus, moss richness does not support Rapoport's elevational rule either.

DISCUSSION

Mid-elevation peak in species richness

Bryophyte richness varies strongly with altitude in Nepal (Figs 1 & 2), similarly to the pattern observed for vascular plants (Grytnes & Vetaas, 2002; Oommen & Shanker, 2005; Bhattarai & Vetaas, 2006) and ferns (Bhattarai *et al.*, 2004). In all cases, the patterns show a mid-elevation peak in species richness. A hump-shaped relationship of bryophyte richness with altitude has also been found in other areas, such as in the tropics (Gradstein & Pocs, 1989; Wolf, 1993). Andrew *et al.* (2003) also reported a unimodal response in some mountains in Tasmania, although it was not general for all sites studied.

When comparing our results to the cross-section of the vegetation in the altitudinal belts of Central Nepal described by

Beug & Miehe (1999), ferns have their maximum richness 100 m below the altitude where the lower cloud-forest belt starts; moss richness peaks exactly at the altitude where the middle cloud-forest belt starts and liverwort richness peaks about 200 m below the lower limit of the upper cloud-forest belt. According to data from Bhattarai *et al.* (2004), vascular plants in Nepal have a maximum richness at around 14–17°C mean annual temperature and 250–330 growing days, whereas ferns have a maximum richness at around 15°C mean annual temperature and 300 growing days. Based on climatic data from Bhattarai *et al.* (2004), we estimate that maximum species richness for mosses occurs at around 13°C and 265 growing days, whereas maximum liverwort richness occurs at around 10°C and 225 growing days.

Maximum liverwort richness is found at lower mean annual temperatures. This coincides with a short growing-season length and high moisture. Liverworts are particularly prevalent in moist and cool habitats (Turner *et al.*, 2006), and our findings support this. The fact that liverworts may require more moisture and can withstand a shorter growing season and low temperatures could be a possible explanation for the altitudinal differences in the species richness peaks of mosses and liverworts.

In order to understand how climate may explain bryophyte richness patterns, it is interesting to relate climate to the evolutionary adaptations of bryophytes. According to Oliver *et al.* (2000), the evolution of terrestrial plants might be a result of changes in desiccation tolerance; as species evolved, vegetative desiccation tolerance was lost as increased growth rates, structural and morphological complexity and mechanisms that conserve water within the plant and maintain efficient carbon fixation were selected for. Oliver *et al.* (2000), after compiling several recent studies, proposed that liverworts were the most primitive group of land plants, and closely related to mosses, whereas mosses were the evolutionary step prior to tracheophytes, such as ferns and vascular plants. Assuming that the driving force of terrestrial plant evolution involved coping better with water stress, vascular plants should be better adapted to water conservation than ferns, which in turn should be better adapted than mosses, which in turn should be better adapted than liverworts. Such different adaptations to water stress may provide some explanations for maximum species richness occurring at decreasing altitudes, starting with liverworts at highest elevations, followed by mosses and finally ferns and vascular plants towards lower altitudes. The order of appearance from higher to lower altitude may reflect the order in which plant species evolved in the past according to the phylogeny presented by Oliver *et al.* (2000). The presumably less-evolved adaptation to water stress in liverworts is associated with higher species richness in areas where potential evapotranspiration (PET), the number of growing days and the mean annual temperature are low, resulting in high moisture. On the other hand, the progressively better adaptations of mosses, ferns and vascular plants to water stress allow them to have peak richness at altitudes with gradually higher number of growing days, mean annual

temperature and PET values, resulting in higher water stress. The decrease in species richness at high altitudes is probably due to ecophysiological constraints, such as reduced growing season, low temperatures, frost susceptibility and low energy (Brown, 2001; Körner, 2003).

One additionally possible important factor for the low species richness at high altitudes is that a high proportion of the Nepalese bryophytes have been described as epiphytes or are associated with logs and fallen trees (Kattel, 2002; H.J.B. Birks, personal observation). Forests in the Nepalese foothills (2500–4000 m) provide a range of habitats for mosses and liverworts including rocks, logs, trunks, branches, twigs and leaves, all of which support bryophytes, especially in the zone of strongest summer rain (up to 4000 mm) between 2500 and 3600 m (Beug & Miehe, 1999). The timberline in the Nepalese Himalaya is around 4000–4300 m (Bhattarai & Vetaas, 2006). At this altitude there is a low bryophyte richness, which suggests that the lack of forests and trees and hence the absence of important habitats may be an important reason for the decreasing bryophyte species richness, as occurs with ferns (Beug & Miehe, 1999; Bhattarai *et al.*, 2004). A marked decrease in bryophyte richness towards the lowlands has also been found in other vegetation types in Nepal (Bhattarai & Vetaas, 2003, 2006; Bhattarai *et al.*, 2004). The very small number of species found in the lowlands may be due to inadequate sampling or, more likely, to habitat loss. Deforestation in the lower part of Nepal started after the control of malaria (Bhattarai *et al.*, 2004), which contributed to extensive habitat loss. However, several plant-hunting expeditions were undertaken prior to extensive deforestation (Bhattarai *et al.*, 2004). In general, the richness and abundance of bryophytes decrease dramatically in the lowlands of Himalaya. We hypothesize that the low bryophyte richness observed here is not only caused by habitat loss and inadequate sampling, but may also have other explanations, for example unfavourable macro- or microclimate, including high PET conditions resulting in lower water availability.

If the mid-domain effect was the sole important variable it would predict that all species groups should show the same pattern. This is not seen in this study, indicating that the mid-domain effect alone cannot explain the observed patterns. Grytnes & Vetaas (2002) argued that hard boundaries, an underlying monotonic trend in species richness, incomplete sampling and the interpolation method may, in combination, underestimate species number at the gradient extremes, which may help to explain the observed pattern in species richness along the altitudinal gradient in the Nepalese Himalaya (Grytnes & Vetaas, 2002). However, the clear peaks in species richness observed for bryophytes do not correspond to any of the simulations made in Grytnes & Vetaas (2002), again indicating that the mid-domain effect may not be important in creating the observed patterns for bryophytes. At broad scales, the influence of the mid-domain effect may be limited and overshadowed by area, temperature or energy-related factors, whereas at intermediate scales the mid-domain effect might offer a better explanation (Oommen & Shanker, 2005).

Differences in scale might be the reason why in some studies the mid-domain effect provides more powerful explanations for observed richness patterns than climatic factors or vice versa.

Endemism

There is no overlap between the peak of maximum endemic liverwort species at 3300 m and the maximum of non-endemic liverwort species at 2700 m, with a striking 600 m difference between the peaks (Fig. 1). Similar results have been found for endemic and non-endemic vascular plant species in Nepal (Vetaas & Grytnes, 2002) and for ferns in Costa Rica (Kluge & Kessler, 2006).

A high degree of isolation generally creates endemism. Isolation is obviously more pronounced at higher altitudes, as the high peaks may function as islands in a 'sea' of lowlands. In the Nepalese lowlands the environment is more similar to the regions surrounding it and species may freely expand their ranges. The vegetation in the lowlands has been strongly influenced by human activity, and endemics may have been differentially extirpated compared with widespread species. Glaciation may add to the isolation effects at higher altitudes and may have acted as a dispersal barrier, and enhanced the physical barriers created by the mountains, thereby providing a mechanism for increased isolation (Vetaas & Grytnes, 2002). In addition, for vascular plants it is known that broad-scale climatic dynamics can facilitate hybridization between previously isolated populations, followed by polyploidy, which may result in new species adapted to conditions following climatic change (Stebbins, 1984). It has been proposed that polyploids have a greater resistance to the severe conditions found at high elevations, which may have promoted endemism at higher altitudes (Vetaas & Grytnes, 2002). There is a high polyploidy ratio among neoendemic vascular plant species both in the Himalaya and elsewhere (Kadota, 1987; Sakya & Joshi, 1990; Nayar, 1996; Solitis *et al.*, 1996). Natcheva & Cronberg (2004) report the existence of polyploidy in hepatics, and suggested that several isolating mechanisms that are recognized in flowering plants may possibly also occur in bryophytes. Bischler & Boisselier-Dubayle (1993) showed that polyploidy also occurs in liverworts with restricted ranges. For these reasons, the same processes that favour polyploidy in vascular plants may also influence the number of endemic bryophytes at higher altitudes in the Himalaya.

On the other hand, it is interesting to note that the highest proportion of endemics (Fig. 4) is found at approximately 4250 m, very close to the timberline in the Nepalese Himalaya, which is at around 4000–4300 m (Bhattarai & Vetaas, 2006). However, the flattening and estimated decrease in the endemism ratio towards the highest altitudes should be interpreted with caution because only a few species are observed at these altitudes, resulting in uncertain estimates of the ratio at these altitudes compared with more species-rich areas.

Rapoport's elevational rule

In some studies, Rapoport's rule has been reported to apply to trees, seaweeds, arthropods, marine and terrestrial molluscs, fish, amphibians, reptiles, birds and mammals (Pianka, 1989; Stevens, 1989; Gaston, 2003; Almeida-Neto *et al.*, 2006; Hausdorf, 2006; Morin & Chuine, 2006). However, Bhattarai & Vetaas (2006) studied tree species richness in Nepal and found no support for Rapoport's elevational rule since altitudinal ranges were narrow at both ends of the gradient and wide at middle elevations. Although altitudinal ranges increase towards higher altitudes according to our data (Fig. 5), this study gives no clear support for Rapoport's rule as proposed by Stevens (1992). The Monte Carlo simulations, which compared the observed correlations for this rule with a null model, showed that such a pattern, which coincides with the predictions from Rapoport's rule, could have been obtained randomly. The null model proposed no significant difference in elevational ranges of mosses and liverworts with altitude, and since we found a 6.3% probability that the null model corresponds to our empirical data we cannot say that Rapoport's rule is supported for the Nepalese liverworts. In addition, the shift between non-endemic and endemic liverwort species (Fig. 1) also does not support Rapoport's elevational rule (Stevens, 1992), which proposes that endemic species should increase towards the lowlands because, by definition, they have a narrow geographical range.

In any case, species ranges result from complex interactions among many factors ranging from physiological traits to the complex history of speciation and dispersal, and constraints resulting from continent shape (Webb & Gaston, 2003). No general trends appear to exist for Rapoport's rule for all biological organisms, suggesting that the factors determining range size are complex and remain poorly understood.

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REFERENCES

- Almeida-Neto, M., Machado, G., Pinto-da-Rocha, R. & Giarretta, A.A. (2006) Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain Rapoport's rule? *Journal of Biogeography*, **33**, 361–375.
- Andrew, N.R., Rodgerson, L. & Dunlop, M. (2003) Variation in invertebrate-bryophyte community structure at different

- spatial scales along altitudinal gradients. *Journal of Biogeography*, **30**, 731–746.
- Beug, H.J. & Miehe, G. (1999) *Vegetation history and human impact in the Eastern Central Himalaya (Langtang and Helambu, Nepal)*. Dissertationes Botanicae 318. J. Cramer, Berlin and Stuttgart.
- Bhattarai, K.R. & Vetaas, O.R. (2003) Variation in plant species richness of different lifeforms along a subtropical elevation gradient in the Himalayas, east Nepal. *Global Ecology and Biogeography*, **12**, 327–340.
- Bhattarai, K.R. & Vetaas, O.R. (2006) Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal? *Diversity and Distributions*, **12**, 373–378.
- Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.A. (2004) Fern species richness along a Central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, **31**, 389–400.
- Bischler, H. & Boisselier-Dubayle, M.C. (1993) Variation in a polyploid, dioicous liverwort, *Marchantia globosa*. *American Journal of Botany*, **80**, 953–958.
- Brown, J.H. (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, Sunderland, MA.
- Chaudhary, R.P. (1998) *Biodiversity in Nepal. Status and conservation*. Know Nepal series, 17. Tecpress Books, Bangkok.
- Colwell, R.K. & Hurr, G.C. (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *The 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 & Evolution*, **15**, 70–76.
- Dobremez, J.F. (1976) *Le Népal, écologie et biogéographie*. Centre National de la Recherche Scientifique, Paris.
- Furuki, T. & Long, D.G. (1994) *Aneura crateriformis*, a new liverwort species from the East Himalaya and China. *Journal of Bryology*, **18**, 281–286.
- Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, New York.
- Gómez, D., Sesé, J.A. & Villar, L. (2003) The vegetation of the alpine zone in the Pyrenees. *Alpine biodiversity in Europe*, Ecological Studies, Vol. 167 (ed. by L. Nagy, G. Grabherr, C. Körner and D.B.A. Thompson) pp. 85–92. Springer-Verlag, Berlin.
- Gradstein, S.R. & Pocs, T. (1989) Bryophytes. *Tropical rain-forest ecosystems: biogeographical and ecological studies*, ecosystems of the World, 14 (ed. by H. Lieth and M.J.A. Werger), pp. 311–325. B. Elsevier, Amsterdam.
- Grolle, R., Schill, D.B. & Long, D.G. (2003) Notes on *Gottschelia* (Jungermanniales, Lophoziales), with a description of *G. patoniae*, a new species from the East Himalaya. *Journal of Bryology*, **25**, 3–6.
- Grytnes, J.A. (2003) Species richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, **26**, 291–300.
- 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. *The American Naturalist*, **159**, 294–304.
- Grytnes, J.A., Heegaard, E. & Ihlen, P.G. (2006) Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. *Acta Oecologica-International Journal of Ecology*, **29**, 241–246.
- Hagen, T. (1969) Report on the geological survey of Nepal. *Denkschrift der Schweizerischen Naturforschenden Gesellschaft*, **LXXXVI/I**, 185.
- Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized additive models*. Chapman & Hall, London.
- Hausdorf, B. (2006) Latitudinal and altitudinal diversity patterns and Rapoport effects in north-west European land snails and their causes. *Biological Journal of the Linnean Society*, **87**, 309–323.
- Kadota, J. (1987) *A revision of Aconitum subgenus Aconitum (Ranunculaceae) of Eastern Asia*. Sanwa Shoyaku Co., Utsunomiya, Japan.
- Kattel, L.P. (2002) *Liverworts of Nepal*. Dambari Kattel Publishing, Kathmandu.
- Kattel, L.P. & Adhikari, M.K. (1992) *Mosses of Nepal*. Natural History Society of Nepal, Kathmandu.
- Kessler, M. (2000) Elevational gradients in species richness and endemism of selected plant groups in the Central Bolivian Andes. *Plant Ecology*, **149**, 181–193.
- Kluge, J. & Kessler, M. (2006) Fern endemism and its correlates: contribution from an elevational transect in Costa Rica. *Diversity and Distributions*, **12**, 535–545.
- Körner, C. (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology & Evolution*, **15**, 513–514.
- Körner, C. (2002) Mountain biodiversity, its causes and function: an overview. *Mountain biodiversity: a global assessment* (ed. by Ch. Körner and E.M. Spehn), pp. 3–20. Parthenon, Boca Raton, FL.
- Körner, C. (2003) *Alpine plant life*, 2nd edn. Springer-Verlag, Berlin.
- Lomolino, M.V. (2001) Elevation gradients of species-richness, historical and prospective views. *Global Ecology and Biogeography*, **10**, 3–13.
- Long, D.G. (1995) The Musci Indica: its authors, types and localities. *Botanical Journal of the Linnean Society*, **119**, 1–33.
- Long, D.G. (1999) Studies on the genus *Asterella*, IV. *Asterella grollei* sp. nov., a new species from Eastern Asia related to the American *A. palmeri*. *Bryologist*, **102**, 169–178.
- Long, D.G. (2005) Notes on Himalayan Hepaticae, 2: new records and extensions of range for some Himalayan leafy liverworts. *Cryptogamie, Bryologie*, **26**, 97–107.
- Long, D.G. (2006) Notes on Himalayan Hepaticae, 3: new records and extension of range for some Himalayan and Chinese Marchantiales. *Cryptogamie, Bryologie*, **27**, 119–129.
- Long, D.G., Paton, J.A., Squirrell, J., Woodhead, M. & Hollingsworth, P.M. (2006) Morphological, ecological and genetic evidence for distinguishing *Anastrophyllum joergensenii*

- Schiffn. and *A. alpinum* Steph. (Jungermanniopsida: Lophoziaceae). *Journal of Bryology*, **28**, 108–117.
- Manandhar, M.S. (1999) Evolution of the Himalaya. *Nepal nature's paradise* (ed. by T.C. Majupuria and R.K. Majupuria), pp. 13–17. Hillside Press Ltd, Kathmandu.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*, 2nd edn. Chapman & Hall, London.
- Morin, X. & Chuine, I. (2006) Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters*, **9**, 185–195.
- Natcheva, R. & Cronberg, N. (2004) What do we know about hybridisation among bryophytes in nature? *Canadian Journal of Botany*, **82**, 1687–1704.
- Nayar, M.P. (1996) *Hotspots of endemic plants of India, Nepal, and Bhutan*. Tropical Botanic Garden and Research Institute, Palode, Thiruvananthapuram.
- Ochra, R. (1989) *Miehea himalayana*, a new species and genus of Hylocomiaceae (Musci) from the Himalayas. *Nova Hedwigia*, **49**, 323–332.
- Ohlemüller, R. & Wilson, J.B. (2000) Vascular plant species richness along latitudinal and altitudinal gradients: a contribution from New Zealand temperate rainforests. *Ecology Letters*, **3**, 262–266.
- Oliver, M., Tuba, Z. & Mishler, B.D. (2000) The evolution of vegetative desiccation tolerance in land plants. *Plant Ecology*, **151**, 85–100.
- Oommen, M.A. & Shanker, K. (2005) Elevational species richness patterns emerge from multiple local mechanisms in Himalayan woody plants. *Ecology*, **86**, 3039–3047.
- Peet, R. (1974) The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5**, 285–307.
- Pianka, E.R. (1989) Latitudinal gradients in species–diversity. *Trends in Ecology & Evolution*, **4**, 223–223.
- R Development Core Team (2004) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Rahbek, C. (1997) The relationship among area, elevation and regional species richness in neotropical birds. *The American Naturalist*, **149**, 875–902.
- Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species–richness patterns. *Ecology Letters*, **8**, 224–239.
- Rey Benayas, J.M.R. (1995) Patterns of diversity in the strata of boreal montane forest in British Columbia. *Journal of Vegetation Science*, **6**, 95–98.
- Sakya, S.R. & Joshi, K.K. (1990) Karyomorphological studies in some *Primula* species of Nepal Himalaya. *Cytologia*, **55**, 571–579.
- Schill, D. & Long, D.G. (2003) A revision of *Anastrophyllum* (Spruce) Steph. (Jungermanniales, Lophoziaceae) in the Himalayan Region and Western China. *Journal of the Hattori Botanical Laboratory*, **94**, 115–157.
- 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. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, **133**, 240–256.
- Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, **140**, 893–911.
- Turner, P.A.M., Kirkpatrick, J.B. & Pharo, E.J. (2006) Bryophyte relationship with environmental and structural variables in Tasmanian old-growth mixed eucalypt forest. *Australian Journal of Botany*, **54**, 239–247.
- Vetaas, O.R. & Grytnes, J.A. (2002) Distribution of vascular plants species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography*, **11**, 291–301.
- Webb, T.J. & Gaston, K.J. (2003) On the heritability of geographic range sizes. *The American Naturalist*, **164**, 553–566.
- Wilbraham, J. & Long, D.G. (2005) *Zygodon* Hook & Taylor and *Bryomaltala* Goffinet (Bryopsida: Orthotrichaceae) in the Sino-Himalaya. *Journal of Bryology*, **27**, 329–342.
- Wolf, J.H.D. (1993) Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Annual Report–Missouri Botanical Garden*, **80**, 928–960.
- Zapata, F.A., Gaston, K.J. & Chown, S.L. (2003) Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology*, **72**, 677–690.
- Zhu, R.–L. & Long, D.G. (2003) Lejeuneaceae (Hepaticae) from several recent collections from the Himalaya. *Journal of the Hattori Botanical Laboratory*, **93**, 101–115.

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