

Can Rapoport's rule explain tree species richness along the Himalayan elevation gradient, Nepal?

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ABSTRACT

Rapoport's rule applied to an elevation gradient predicts a positive correlation between elevation ranges and elevation. This is supposed to be caused by the increasing magnitude of the climatic extremes at higher elevations, and thus, it is deduced that species richness should decrease with increasing elevation. The distribution of 614 tree species was used to test Rapoport's elevational rule along a gradient from 100 to 4300 m a.s.l., in the Nepalese Himalaya. The relationship between species richness and elevation was analysed by using generalized linear models (GLM). Generalized additive models (GAM) were used to examine the relationship between elevational range and the elevational mid-point of a species along the gradient. The widest elevation ranges are observed at mid-elevations, and narrow elevation ranges are observed at both ends of the gradient. This does not support Rapoport's elevation rule, as proposed by Stevens. There is a peak in species richness between 900 and 1000 m, and not in the tropical lowland as projected by Rapoport's elevation rule.

Keywords

Elevation, elevation range, generalized linear models, Nepal, Rapoport's rule, species richness, unimodal relationship.

INTRODUCTION

Regional variation in species richness is the subject of long-standing debates in ecology and biogeography (see Piank, 1966; Huston, 1994; Lomolino, 2001; Whittaker *et al.*, 2001). The variation of species richness along elevation gradients has been documented for a variety of taxa and geographical areas (e.g. Terborgh, 1977; Stevens, 1992; Rahbek, 1995, 1997; Brown, 2001; Heaney, 2001; Md. Nor, 2001; Bhattarai & Vetaas, 2003, 2005; Grytnes, 2003; Bhattarai *et al.*, 2004; Carpenter, 2005). Two general patterns have emerged: a monotonic decrease in species richness (e.g. Yoda, 1967; MacArthur, 1972; Stevens, 1992); or a hump-shaped relationship with a peak in species richness at intermediate elevations (e.g. Grytnes & Vetaas, 2002). From a review of the literature, Rahbek (1995) concluded that hump-shaped relationships are most common in both tropical and non-tropical biomes.

Many hypotheses have been proposed to explain the variation in species richness along elevational gradients. One hypothesis proposes that there is a positive correlation between elevation and the elevational range of species. This pattern has been called Rapoport's elevation rule (Stevens, 1992), derived from earlier work on latitudinal gradients by Rapoport (1975, 1982), that found that latitudinal ranges of species increase with increasing latitude (Rapoport, 1982; Stevens, 1989). Rapoport's elevation

rule arises as a result of the ever-narrowing range of climatic conditions that species experience with decreasing elevation (Stevens, 1992). It suggests that species occurring at higher elevations must be able to withstand a broad range of climatic conditions and this leads to a wide elevation range. Species found at lower elevations are adapted to more specific temperature and rainfall conditions so they have narrow climatic tolerances and hence a smaller range, resulting in more species. Patterns consistent with Rapoport's rule have been documented for trees, mammals, amphibians, grasshoppers, and reptiles (Stevens, 1992 and references therein).

Colwell and Hurt (1994) proposed a new hypothesis called 'hard boundary' or 'mid-domain effect' to explain mid-elevational peaks in species richness. They suggested 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. Contrary to Rapoport's rule, the hard boundary hypothesis predicts that species ranges at higher elevations are narrow.

Although Rapoport's elevation rule has been suggested to explain decreasing species richness towards higher elevations, this has been debated in many studies (e.g. Rohde, 1992; Rohde *et al.*, 1993; Colwell & Hurt, 1994; Fraser *et al.*, 1994; Smith *et al.*, 1994; Rohde, 1996; Gaston *et al.*, 1998; Kerr, 1999). The aim of

this study was to test whether Rapoport's elevation rule can explain the variation in tree species richness along the elevational gradient in the Himalayas. The Himalayas have the longest bioclimatic gradient in the world and offer an excellent site to test such a hypothesis. There is always a degree of uncertainty in the range data used for these types of analyses, but range data are feasible to elucidate patterns in elevation richness (Rowe, 2005). We used trees because they may be more influenced by climate than herbaceous species (Bhattarai & Vetaas, 2003), and elevation ranges for trees are more accurate than for smaller plants.

METHODS

Location of study area and its vegetation

The study covers the central Himalayas, Nepal (26°22' to 30°27' N and 80°4' to 88°12' E), an area 800 km east–west by 150–200 km north–south. The Indo-Gangetic plain is to the south of the Himalayan range. In the northern part of the Indo-Gangetic plain there is a 30–40 km wide flat area, which is called Terai in Nepal. North of this flatland, the Siwalik hills rise abruptly to an average elevation of 1300 m. This mountain system is composed of sedimentary rock of Oligocene to Pleistocene age (Hagen, 1969). The Mahabharat range or the Lesser Himalaya forms the mid-hills of Nepal and elevation rises from 1500 to 3000 m. It controls the climate of the midland of Nepal and is composed of hard rocks like granite and limestone (Hagen, 1969; Pandey, 1995). North of the Mahabharat range are the Great Himalayas (5000–8000 m), with some of the highest peaks in the world. The Himalayan range grades into the Tibetan Plateau to the north, i.e. Trans-Himalayan zone, with a climate and vegetation similar to that of the Tibetan Plateau.

The Himalayan elevation gradient extends from *c.* 60 to > 8000 m within 150–200 km and includes compressed tropical/subtropical, temperate, subalpine, and alpine climatic zones. Up to 1000 m there is a tropical or subtropical zone 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*. In the cool temperate zone (2000–3000 m), the forest is dominated by laurel, oak, and *Rhododendron* stands. The subalpine zone (3000–4000 m) is dominated by *Betula utilis* and coniferous forest. The upper elevation limits for *Abies spectabilis*, *Pinus wallichiana*, and *B. utilis* forest are 4000–4300 m (Stainton, 1972).

Data sources, interpolation, and area

This is a broad-scale study covering the whole Himalayan elevation gradient. We have used the secondary data source of Press *et al.* (2000), which is an elaborated version of the *Enumeration of the Flowering Plants of Nepal* (Hara *et al.*, 1978, 1982; Hara & Williams, 1979). This is a most reliable and up-to-date source about the flora of Nepal and is based on extensive field studies, reviews of published literature, and examinations of herbaria. It provides information on 614 tree species growing from 80 m

a.s.l. to the tree line. Those tree species whose distribution range is only crudely mentioned are not included here. To examine the relationship between species richness and elevation, the total elevation gradient between 100 and 4400 m was divided into 43,100-m elevation intervals (vertical elevation band). The number of species present in each band is estimated by the interpolation method. A species was defined as being present in every 100-m interval between its upper and lower elevation limits. For example, *Bombax ceiba* L., with its elevation limit between 200 and 900 m, was assumed to be present in each elevation band of 200, 300, 400, 500, and so on up to 900 m (see Patterson *et al.*, 1996, 1998; Rahbek, 1997; Fleishman *et al.*, 1998; Brühl *et al.*, 1999; Grytnes & Vetaas, 2002; Vetaas & Grytnes, 2002). The term species richness is defined as the total number of tree species found in each 100 m elevation band, which has been called gamma diversity by Lomolino (2001).

The elevation range of each species was estimated as the difference between the maximum and minimum elevations where a species was found within the range of survey sites, rounded off to the nearest 100 m (see Stevens, 1992; Colwell & Hurt, 1994; Fleishman *et al.*, 1998; Sanders, 2002; Bhattarai & Vetaas, 2005). Species reported from a single site were given an elevational range of 100 and were also included in the analysis. The mid-point of a species at a given site was calculated by averaging the lowest and highest elevation limits of each species present (Stevens, 1992).

We also analysed the relationship between available area and species richness. We used data on area prepared by the Integrated Centre for Mountain Development (ICIMOD, Kathmandu, www.icimod.org.np) based on digitized maps of Nepal at 500-m contours. Estimates of area are available for each 500-m elevation band and are used here to examine species richness area relationships for each 500-m elevation band (cf. Vetaas & Grytnes, 2002).

Numerical analysis

We used least square regression to analyse the species–area relationship. We used generalized linear models (GLM; McCullagh & Nelder, 1989; Dobson, 1990) to examine the relationships between tree richness and elevation. The response variable, species richness, is a discrete data type (counts) and may follow a Poisson error distribution (McCullagh & Nelder, 1989), which requires a logarithmic link. A GLM model was generated with a logarithmic link and also one with an identity link function. The difference between a logarithmic link and an identity link function (which assumes a normal error distribution) was assessed by Q-Q diagnostic plots of the residuals from preliminary tests (Crawley, 1993; Hastie & Pregibon, 1993). Although the counts were high (tree species) and the error distribution was almost indistinguishable from normal, we chose the Poisson model because of the nature of the response variable (Crawley, 2002). The models were checked with up to third-order polynomial regressions. We used an *F*-test to check the significance of models, because this is more robust than the chi-squared test when models are over-dispersed (Crawley, 2002).

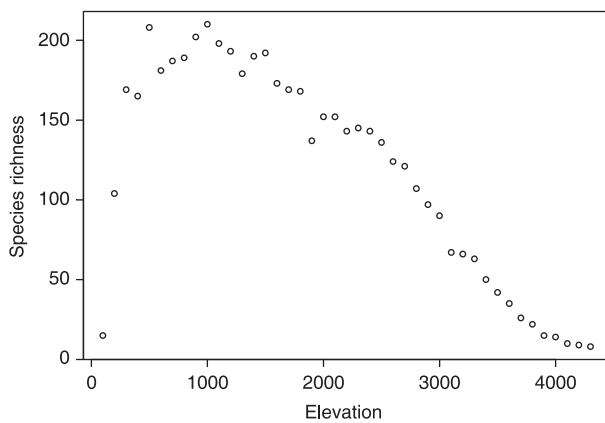


Figure 1 Plot showing the relationship between tree species richness and elevation (m).

Table 1 Summary of regression statistics when species richness is regressed against elevation. Polynomial first (1) and second (2) order models were tested against the null model and each other. The deviance explained indicates the percentage of total (null) deviance (2056)

| Variables | Degrees of freedom | Polynomial order | Res. dev. | % Dev.expl. | P-value |
|-----------|--------------------|------------------|-----------|-------------|-------------|
| Elevation | 41 | 1 | 1011.7 | 51 | $P < 0.001$ |
| Elevation | 40 | 2 | 217.9 | 89 | $P < 0.001$ |

Res.dev. = residual deviance; Dev.expl. = deviance explained.

To examine the relationship between the elevational mid-point and elevational range, a smoother was fitted by generalized additive modelling (GAM) with 4 d.f. (Hastie & Tibshirani, 1990). GAM allows the data to determine the shape of the response curve instead of being limited by shapes available in parametric regression (Crawley, 2002), but the fitted line is only to aid the reader's eye; it is not meant to imply any causality. The series of elevational ranges and elevational mid-points of species along the gradient do not indicate any independence of the data set (Gaston *et al.*, 1998), and so a more detailed analysis of the scatter of points is not statistically meaningful (Stevens, 1992). We used s-PLUS (version 6.1) for all the regression analyses and graphical representations.

RESULTS

A total of 614 tree species (excluding those whose distribution range is poorly described) is reported growing from 80 m up to the timber line in the Nepal Himalaya (i.e. 4300 m), which comprises about 12% of the total flora of Nepal. There are a few tree species (*A. spectabilis*, *Juniperus squamata*, and *Salix daltoniana*) that have distributions up to 4400 m a.s.l., and *Juniperus recurva* and *Salix bhutanensis* have been reported above the timber line up to 4600 m a.s.l., some of the highest tree occurrences.

Tree species richness increases up to 1000 m and decreases afterwards, showing a mid-elevation peak in richness (Fig. 1,

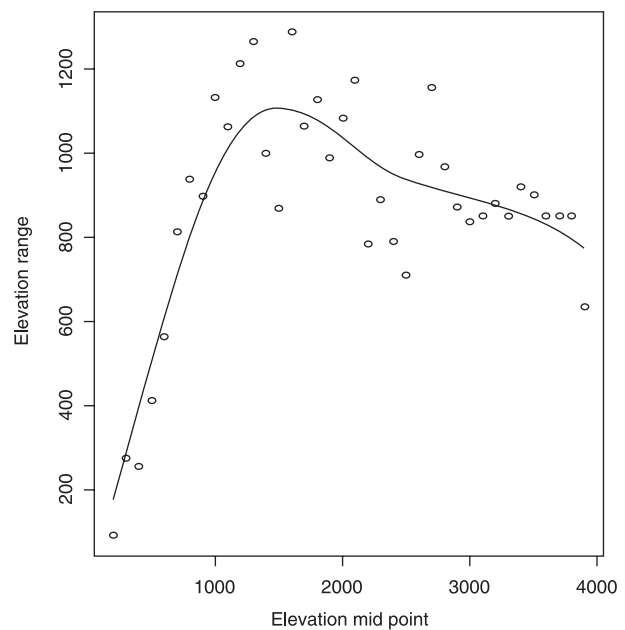


Figure 2 Plot showing the relationship between elevation range and elevation mid-point (m). The line is fitted by generalized additive models with four degrees of freedom, and line is fitted to guide the reader's eye.

Table 1). The elevational range of species increases from 100 to 1500 m as Rapoport's elevation rule predicts. Above 1500 m elevational ranges decrease; however, contrary to the elevational Rapoport effect proposed by Stevens (1992). Thus, there is a narrow elevation range at lower elevations, a wider elevation range at the middle of the gradient and, slightly narrower ranges at higher elevations (Fig. 2). The correlation between elevational mid-point and elevational range is not significant along the whole gradient. However, there is a strong positive correlation up to 1500 m (d.f. = 14, $r = 0.88$, $P < 0.01$) and a significant negative correlation above 1500 m (d.f. = 23, $r = -0.64$, $P < 0.01$).

The relationship between elevation and area estimated for each 500 m elevation level is shown in Fig. 3. The area decreases monotonically with increasing elevation. There is a linear relationship between log-area and tree richness (Fig. 3), but there is a drop in richness at lower elevations where the area is largest.

DISCUSSION

This study found a peak tree richness in the lower half of the elevational gradient, which is consistent with the results from several other studies (e.g. Terborg, 1977; Md. Nor, 2001; Grytnes & Vetaas, 2002). Rahbek's (1995) review concluded that the mid-elevation peak is a common pattern. This study did not find monotonically decreasing tree species richness with increasing elevation, as suggested by Stevens (1992) and estimated by Yoda (1967) for the Himalayas. Stevens (1992) predicts that elevational range will increase with increasing elevation due to the wider climatic tolerances of high-altitude species. Our results show narrow elevational ranges at both ends of the gradient and

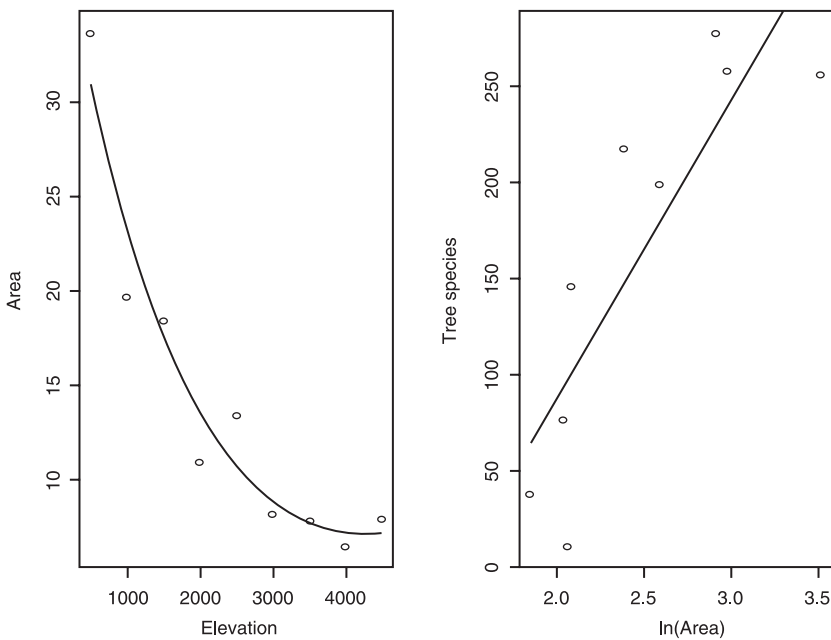


Figure 3 (a) Plot showing the relationship between (area, 1000 km²), and elevation (m). The line is fitted by generalized additive models with three degrees of freedom. (b) Plot showing the linear relationship between area in logarithmic scale (1000 km²), and tree species richness. $R^2 = 0.71$; $F = 17.9$; $P < 0.004$.

a wider elevation range in the middle (Fig. 2). Therefore, Rapoport's elevation rule as proposed by Stevens (1992) receives no overall support from this study. Vetaas and Grytnes (2002) came to a similar conclusion, namely that species at higher elevations in the Himalayas have narrow elevational ranges, which is indirectly indicated by the maximum richness of endemic species at higher elevations.

There are narrow elevation ranges of species at the lower end of the gradient, in partial agreement with Rapoport's elevation rule. This may be due to microhabitat requirement of tropical species (Stevens, 1992), but it may also be an artefact. Interpolation close to the lower end of the gradient may create artificially narrow ranges due to low sampling intensity and hard boundaries (Grytnes & Vetaas, 2002; Grytnes, 2003). When elevational ranges below 500 m are discarded, the ranges at mid-elevations are still wider than those at 500 m a.s.l. This may indicate that after accounting for the interpolation effects, there is partial support for the idea that tropical lowland species have narrow ranges, but the elevational rule has no support. However, larger ranges found at mid-elevation zones support the predictions deduced from the hard boundary model. The hard boundary theory has been criticized by several authors (e.g. Hawkins & Diniz-Filho, 2002; Laurie & Silander, 2002; Zapata *et al.*, 2003) for its non-biological assumptions. But some authors (e.g. Colwell & Hurt, 1994; Colwell & Lees, 2000; Grytnes & Vetaas, 2002; Grytnes, 2003) argue that the mid-elevation peak in species richness will, to various degrees, be related to the dispersal limitations at the gradient endpoints. They argued that the extent of the elevation ranges of species is bounded by hard boundaries present at the tops of mountains and by the sea or valleys at the bottom of the gradient, and expect the range to be wider at mid-elevations and narrower at the gradient endpoints. The peak in tree species richness around 1000 m a.s.l. (Fig. 2) may result therefore from large-scale mass effects, with species from the

tropical zone below 1000 m and the temperate zone from 1000 to 3000 m a.s.l. (Shmida & Wilson, 1985), both providing disjuncts. Thus, mass effects or source-sink dynamics may influence the species richness pattern within an elevational gradient (Grytnes & Vetaas, 2002).

Maximum tree species richness is different from the maximum total species richness (including herbs, shrubs, and trees) found by Grytnes and Vetaas (2002) along the same gradient. They found maximum flowering plant species richness between 1500 and 2500 m. This discrepancy might be associated with different limits of distribution, i.e. different hard boundaries for tree species and non-tree species. Herbaceous species in the Himalayas are reported up to 6500 m (Miehe, 1989), but tree species hardly extend beyond 4300 m, i.e. the timber line. However, if the mid-domain effect or mass effect was the main explanation, one would expect a peak in tree richness at 2100 m a.s.l. (midpoint between 100 and 4300 m a.s.l.). Thus the peak found at c. 1000 m a.s.l. must have an environmental explanation.

Climate is an obvious explanation for a mid-elevation peak in richness (e.g. Odland & Birks, 1999; Md. Nor, 2001). Although estimation of species richness directly from point samples may produce different results from those based on interpolation, an empirical study by Bhattarai and Vetaas (2003) showed good agreement. Along a transect between 100 and 1500 m a.s.l. Bhattarai and Vetaas (2003) found maximum tree species richness around 800 m a.s.l., which is close to the estimated peak in this study. Bhattarai and Vetaas (2003) proposed a climatic explanation, partly in agreement with the model by O'Brien and colleagues (O'Brien, 1993, 1998; Whittaker *et al.*, 2001). They have shown that, in general, tree species richness can be predicted by a linear function of rainfall and a parabolic function of energy. Rainfall is not a simple linear function of elevation, and there is great variation within the same elevation zone (Dobremez, 1976). The stations with highest rainfall are above 500 m

and below 2000 m, but the number of rainy days is highest at 2000 m. Above 1300 m a.s.l. frost occurs in winter and available energy will gradually be reduced at higher elevations (Bhattarai *et al.*, 2004). One would thus expect maximum tree richness to fall between 500 and 1300 m a.s.l., which the estimated tree richness maximum does.

Generally, a larger area supports more species than a smaller area (e.g. Rosenzweig, 1995). Areal extent below 500 m is nearly two to three times larger than all other zones, and above 500 m it decreases steadily until 4000 m a.s.l. (Fig. 3a). There is a significant linear species–area relationship (Fig. 3), although the peak in tree richness at 1000 m is not in the elevation zone with largest area, i.e. below 500 m. However, the data points are few, and subsequently the statistical power is low. Vetaas and Grytnes (2002) did not find a significant linear species–area relationship for total species number along the same gradient. It was argued that 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 (cf. Lomolino, 2001). However, it may be easier to verify the well documented species–area relationship (e.g. Rosenzweig, 1995) for larger organisms such as trees as opposed to a composite group such as flowering plants that include numerous very small species.

In conclusion, high tree species richness seems to occur in elevation zones with large areal extent, relatively high rainfall, but no frost, which in the Himalaya correspond with the transition zone from tropical forest to warm temperate forest. Steven's elevational Rapoport rule was not verified and does not offer a satisfactory explanation for the richness pattern observed. Wider elevation ranges were found at mid-elevations, corresponding with the theory behind the mid-domain effect.

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