

# Species Richness and Altitude: A Comparison between Null Models and Interpolated Plant Species Richness along the Himalayan Altitudinal Gradient, Nepal

John Arvid Grytnes<sup>1,\*</sup> and Ole R. Vetaas<sup>2,†</sup>

1. Department of Botany, University of Bergen, Allégaten 41, N-5007 Bergen, Norway;

2. Centre for Development Studies, University of Bergen, Stroemgaten 54, N-5007 Bergen, Norway

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**ABSTRACT:** We compare different null models for species richness patterns in the Nepalese Himalayas, the largest altitudinal gradient in the world. Species richness is estimated by interpolation of presences between the extreme recorded altitudinal ranges. The number of species in 100-m altitudinal bands increases steeply with altitude until 1,500 m above sea level. Between 1,500 and 2,500 m, little change in the number of species is observed, but above this altitude, a decrease in species richness is evident. We simulate different null models to investigate the effect of hard boundaries and an assumed linear relationship between species richness and altitude. We also stimulate the effect of interpolation when incomplete sampling is assumed. Some modifications on earlier simulations are presented. We demonstrate that all three factors in combination may explain the observed pattern in species richness. Estimating species richness by interpolating species presence between maximum and minimum altitudes creates an artificially steep decrease in species richness toward the ends of the gradient. The addition of hard boundaries and an underlying linear trend in species richness is needed to simulate the observed broad pattern in species richness along altitude in the Nepalese Himalayas.

**Keywords:** hard boundaries, interpolation, null model, unimodal relationship.

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The latitudinal decrease in species richness has been known for over a century (Wallace 1878; Pianka 1966; Brown and Lomolino 1998). This latitudinal pattern is commonly explained by a monotonic relationship with

climatic factors such as primary productivity or other energy-related factors (Richerson and Lum 1980; Turner et al. 1987; Currie 1991; Rohde 1992; Wright et al. 1993; Austin et al. 1996; Grytnes et al. 1999). Altitudinal trends in species richness are generally thought to mimic latitudinal trends in species richness, and the same factors are often used to explain this altitudinal pattern (MacArthur 1969, 1972; Begon et al. 1990; Rohde 1992; Rahbek 1997; Brown and Lomolino 1998; Givnish 1999). Several studies have found a decreasing trend in species richness with altitude (e.g., Yoda 1967; Alexander and Hilliard 1969; Kikkawa and Williams 1971; Hamilton 1975; Hågvar 1976; Wolda 1987; Gentry 1988; Kitayama 1992; Navarro 1992; Stevens 1992; Patterson et al. 1998; Vazquez and Givnish 1998; Odland and Birks 1999).

Rahbek (1995) presented a critical literature review on species richness patterns in relation to altitude and showed that approximately half of the studies detected a mid-altitude peak in species richness. Studies finding a humped relationship between species richness and altitude include Whittaker (1960), Janzen (1973), Whittaker and Niering (1975), Shmida and Wilson (1985), McCoy (1990), Lieberman et al. (1996), Gutiérrez (1997), Rahbek (1997), and Fleishman et al. (1998).

A recently recognized factor that may contribute to a humped relationship between species richness and altitude is the geometric constraint on species ranges (Pineda 1993; Colwell and Hurtt 1994; Rahbek 1997; Pineda and Caswell 1998; Lees et al. 1999; Colwell and Lees 2000). The range of a species along an altitudinal gradient is geometrically constrained by sea level or the bottom of a valley as a lower boundary and the top of a mountain or an eco-physiological constraint as an upper boundary. If these boundaries present some degree of resistance to dispersal, they form so-called hard boundaries (Colwell and Lees 2000). Simulations and analytical modeling have shown that hard boundaries alone (given a random distribution of species) can cause a unimodal relationship between species richness and vertical or horizontal gradients (Colwell

\* Corresponding author; e-mail: jon.grytnes@bot.uib.no.

† E-mail: ole.vetaas@bot.uib.no.

and Hurtt 1994; Pineda and Caswell 1998; Willig and Lyons 1998; Lees et al. 1999; Colwell and Lees 2000).

Different aspects of sampling may also seriously affect the observed species richness pattern along altitude (Terborgh 1977; Wolda 1987; McCoy 1990; Colwell and Hurtt 1994; Rahbek 1997). One little-acknowledged factor is that patterns may seriously be affected by how species richness is estimated. Estimations of species richness directly from point samples may produce different results from those based on the assumption that species are present at all altitudes between the extremes at which they have been observed. Such interpolation may result in an underestimation of species richness at the extreme altitudes compared with the midaltitude areas. This is clearly seen when considering the two extreme altitudinal bands. Here, only the species that have actually been observed are counted. For all other bands, interpolated species not observed in the actual band are added to the species observed, which results in an overestimation of species richness at mid-altitudes compared with extreme altitudes. Overestimation is avoided only if all the observed maxima and minima are true and all species are present in all bands between the extremes. Although many species richness studies are based on interpolated species distributions, the effect of this interpolation has not previously been tested.

The aim of this article is to investigate how hard boundaries, interpolation together with incomplete sampling, and an underlying linear trend in species richness influence the species richness relationship with altitude by simulating different null models. We first describe the altitudinal species richness pattern in Nepal and then discuss how well the different null models can simulate the observed species richness patterns.

### Empirical Data

The Himalayan elevation gradient is the longest bioclimatic gradient in the world, and vascular plants in Nepal are found from 60 to 6,400 m above sea level (a.s.l.). Within only 150 km, one moves from the tropical zone to the nival zone with permanent frost and snow. There is a tropical climate on the southern plateau in Nepal (Terai) up to around 1,000 m. Between 1,000 and 2,000 m, the subtropical or warm-temperate zone is found. Above this and up to approximately 3,000 m, the cold-temperate zone dominates. The highest limit of the overlying subalpine zone, which is between 4,000 and 4,500 m, defines the tree limit in Nepal. In the alpine zone, there are some shrubs, but grassland is predominant. In the high-alpine zone, the vegetation is more discontinuous (Dobremetz 1976).

The three volumes of *An Enumeration of the Flowering Plants of Nepal* (Hara et al. 1978, 1982; Hara and Williams

1979) report the lower and upper altitude limits for 4,928 taxa (of the approximately 6,000 species mentioned). This is based on over 100,000 herbarium specimens in addition to the field experience of the authors and others (Hara et al. 1978). A small number of taxa are subspecies or other subspecific rank. "Observed species richness" refers here to interpolated taxonomic richness based on this total data set.

We divided the elevation gradient between sea level and 6,000 m a.s.l. into 60 100-m vertical bands (excluding the occurrences of four species above 6,000 m). A species was assumed to be present in each 100-m band between its upper and lower altitude limits. The upper limit of the altitude band is used to define each band; for example, a species with its altitudinal limits between 410 and 600 m is then present in the 500- and 600-m bands. This method of interpolating species presence between the extreme altitudes has commonly been used to investigate species richness patterns along altitude in regional and continental studies (e.g., Patterson et al. 1996, 1998; Rahbek 1997; Fleishman et al. 1998; Brühl et al. 1999; Odland and Birks 1999).

### Simulations

The species richness patterns along the altitudinal gradient are simulated using three parameters: species optima, species range, and probability of sampling species in altitude bands where they are actually present. The different null models are generated by manipulating these parameters in different ways and combinations. Below, we first explain how the three parameters are manipulated and then how they are combined to generate the different null models (table 1). A pictorial explanation of the simulation procedures is given in figure 1.

#### *Optima and Range Manipulation*

The null models made here are inspired by earlier simulations performed to elucidate the effect of hard boundaries (Colwell and Hurtt 1994; Colwell and Lees 2000). Previous simulations have focused on the actual range of species within the domain or study area and the midpoint of this range (reviewed in Colwell and Lees 2000). These two variables are dependent. Rather than randomizing the actual midpoint and the actual range, we choose the potential range and the potential midpoint (optimum) as our focus for simulation. Ecologically, the species optimum is the altitudinal interval where it has its maximum abundance, and abundance will decrease in both directions away from the optimum (Whittaker 1967). The potential range is here assumed to be independent of the optimum. The part of the potential range of a species that is outside the domain is deleted (fig. 1,  $S_1$  and  $S_2$ ). What is left is the actual range. This will not be symmetric around the

**Table 1:** Overview of how the optimum is simulated to make the different models

	Optimum restriction	Optimum distribution	Simulating
Model 0	–2,500 to 8,500	Uniform	No hard boundaries
Model I	–2,500 to 6,000	Uniform	Upper hard boundary
Model II	0–6,000	Uniform	Two hard boundaries
Model III	–2,500 to 6,000	Linear trend	Upper hard boundary and underlying linear trend in species richness
Model IV	0–6,000	Linear trend	Two hard boundaries and underlying linear trend in species richness

Note: Optimum is simulated as an integer between the values specified in the optimum restriction column and with the distribution specified in the optimum distribution column. The last column describes what the model is simulating.

optimum when the potential range is cut off, and hence the actual midpoint will be different from the optimum simulated (fig. 1). Note that this procedure will, like previous simulations, create a dependency between the actual midpoints and actual ranges toward the ends of the gradient. However, the randomized variables (optimum and potential range) are independent along the whole gradient. Randomizing the optimum and potential range instead of the actual midpoint and actual range will give different species richness patterns and will, in our view, give different ecological interpretations for the hard boundary null models (see “Results” and “Discussion”).

Species richness is simulated in the following way. First, all simulations start with 10,000 species. Second, for each species, an altitudinal optimum is simulated to be an integer between two specified altitudes (differing for different models; see table 1). Optimum is distributed either uniformly or with a linearly decreasing probability function with altitude (table 1). Third, the potential range of a species is simulated to be an integer between 0 and 5,000, which gives the simulated ranges the same maximum as in the empirical data. Different distributions for the ranges had only a minor influence on the species richness patterns and are not considered further. Fourth, the maximum and minimum altitude for a species is found as the optimum  $\pm$  range/2, and the species is interpolated as present at all altitudes between the minimum and maximum altitude. Finally, the number of species is counted in 100-m altitude bands in the same way as for the empirical data. The resulting number of species in each altitudinal band is hereafter called the “simulated actual species richness.”

#### *Manipulation of the Proportion of Species Sampled*

An implicit assumption when species richness estimates are based on interpolated species distributions is that all observed extremes define the correct end points of the range of the species. The data source used here is mainly based on herbarium specimens. In such data, it is reason-

able to assume that the true extremes are not correctly observed for all species. To illustrate how interpolation of such data may influence species richness patterns, we simulate a model in which the observed ranges of the species are based on incomplete sampling. We arbitrarily assume that there is a 20% probability of sampling a species in an altitude band where it is present. This is done by the following procedure.

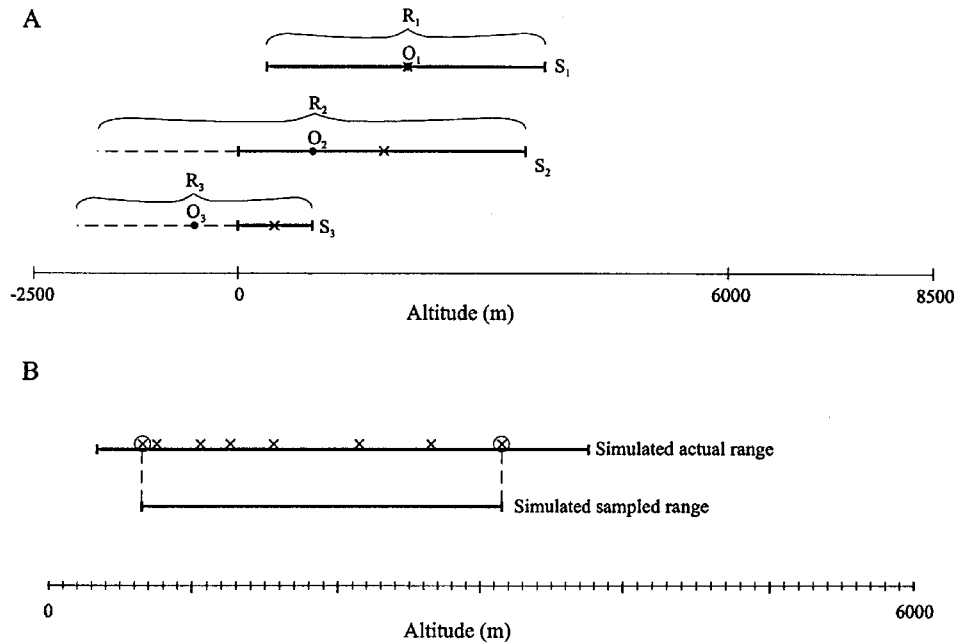
First, the altitudinal distribution of the 10,000 species resulting from the simulations of optima and ranges (described above) are used as a basis. Second, each of the 100-m altitude bands where a species is present is set to have a 20% probability of being sampled. Third, between the new maximum and minimum sampled altitude, a new interpolation is done defining the species as present in all bands between the new extremes (fig. 1). Finally, the resulting species richness pattern, based on interpolation of the sampled extremes and counted in the same bands as above, is referred to as the “simulated sampled species richness.”

#### **Null Models**

Five main null models are generated based on combinations of different restrictions or assumptions about the distribution of the species optima. For each of these five models, two submodels with or without complete sampling are made. The null models are summarized in table 1.

##### *Model 0: No Hard Boundaries*

This null model has a uniform distribution of optima along the altitudinal gradient and has no hard boundaries. To obtain this, we extended the gradient by 2,500 m at the lower and upper parts of the gradient (2,500 m is the maximum distance from the optimum when the maximum range is 5,000 m). This means that the theoretical optima may lie between 2,500 m below sea level (b.s.l.) and 8,500 m a.s.l., which allows species with optima beyond the hard boundaries to affect species richness. The



**Figure 1:** Methods used in the simulations. We suppose that there are 10,000 species  $S_i$  ( $i = 1, 2, 3, \dots, 10,000$ ). The randomizations of actual species distributions are shown for three species in A ( $S_1$ – $S_3$ ). The sampling and reinterpolation of one species ( $S_i$ ) are shown in B. A, Each species is specified by its optimum ( $O_i$ ) and potential range ( $R_i$ ), which are randomly chosen as follows: (1)  $O_i$  is an integer where the restriction and distribution depend on the model (table 1), (2)  $R_i$  is an integer between 0 and 5,000, (3) each species  $S_i$  is defined as present between maximum altitude ( $O_i + R_i/2$ ) and minimum altitude ( $O_i - R_i/2$ ), and (4) if the minimum falls below 0, it is defined as 0, and likewise, if the maximum is above 6,000, it is defined to be 6,000. The remaining part is called the actual range (*unbroken line*), and the midpoint of the actual range is the actual midpoint (x). Note that for null models with hard boundaries,  $S_3$  is not possible (see table 1). B, Sampling is simulated by sampling the 100-m altitude bands within the actual range of the species with a probability of 20%. The sampled bands are shown by x's. The highest and lowest bands sampled define the new extremes (*circled x*), and the species are interpolated as present between these new extremes, which results in the simulated sampled ranges. See text for further explanation.

approach used for this model is similar to the methods used to derive model 1 in Colwell and Hurtt (1994). If the optimum for a species is placed at 1,000 m b.s.l., it may influence the species richness pattern in the study area if the range associated with that species is above 2,000 m. Including such species can be justified by assuming that there are climatic conditions corresponding to altitudes below sea level to the south of this area, for example, that there are warmer areas than at the lowest point in Nepal southward on the Indian subcontinent. Species having their optima in these areas may still be able to grow in parts of Nepal. It is more doubtful whether the same argument can be used for the upper part. There are certainly areas, both within and outside Nepal, that have a climate more severe than at 6,000 m a.s.l., but this is probably close to the physiological limits for plant life (Grabherr et al. 1995; Körner 1999). Whether this null model incorporates the “nuldest” biological assumptions is therefore unlikely for the upper boundary and uncertain for the lower boundary. However, including this model

makes the biological assumptions behind the remaining null models much clearer.

#### Models I and II: Hard Boundaries

Previous null models simulating hard boundaries (e.g., Colwell and Hurtt 1994, reviewed in Colwell and Lees 2000) set restrictions on the actual range in the randomizations because species are allowed to appear only when the midpoint of the species is more than half the range size away from the domain boundaries. Our approach sets the restrictions imposed by the hard boundaries on the optima only and not on potential range size.

Hard boundaries are either set at 6,000 m a.s.l. only (i.e., similar to the hybrid model of Colwell and Hurtt [1994]) or at both extremes of the altitude gradient. The upper boundary is probably close to the physiological limit for plant survival, and a hard boundary here is therefore ecologically sound. An ecological justification for the lower hard boundary is that species with optima south of the study

area will have long dispersal distances and hence low probabilities of occurring along the studied gradient. Restricting the optima between 2,500 m b.s.l. and 6,000 m a.s.l. simulates an upper hard boundary only (Model I). Restricting the optima between 0 and 6,000 m a.s.l. simulates the effect of two hard boundaries (Model II).

#### *Models III and IV: Linear Underlying Trend and Hard Boundaries*

These null models simulate the effects of an underlying trend of decreasing species richness with altitude in combination with hard boundaries. This is done by making the probability distribution of species optima dependent on altitude. As a first approximation, we chose to base the probability distribution on a linear regression between altitude and observed species richness between 2,500 and 3,500 m a.s.l. (species richness =  $1,667.8 - 0.1845 \times \text{altitude}$ ). This is because the altitudinal bands between 2,500 and 3,500 m a.s.l. are probably least influenced by the hard boundaries and are assumed to describe the possible underlying trend best. Models III and IV combine this underlying trend of species optima with an upper hard boundary (Model III) and with two hard boundaries (Model IV).

#### *Interactions between Hard Boundaries and Interpolation Method*

With the approach used here, the actual range sizes of species toward the extremes will be less than for species in the middle of the gradient. To evaluate what this means for species richness estimated by interpolation, we compare simulated sampled species richness and simulated actual species richness for Model 0 (no hard boundaries) and Model II (two hard boundaries). Model 0 allows optima to go outside the domain, and the actual ranges will decrease toward the extreme altitudes for this model more than for the Model II (with two hard boundaries).

### **Results**

The observed species richness (based on interpolating species extremes from the literature) shows a unimodal response to altitude in the Nepalese Himalayas. Maximum species richness is found between 1,500 and 2,500 m a.s.l. (fig. 2). Here, species richness varies between 1,140 and 1,271 at 1,900 and 2,400 m a.s.l., respectively. From 100 to 1,500 m a.s.l., species richness increases steeply with altitude, whereas above 2,500 m a.s.l., species richness decreases toward 6,000 m a.s.l. In the lowest altitudinal band between 0 and 100 m, only 62 species are recorded. This is very low compared with the next altitudinal band (with

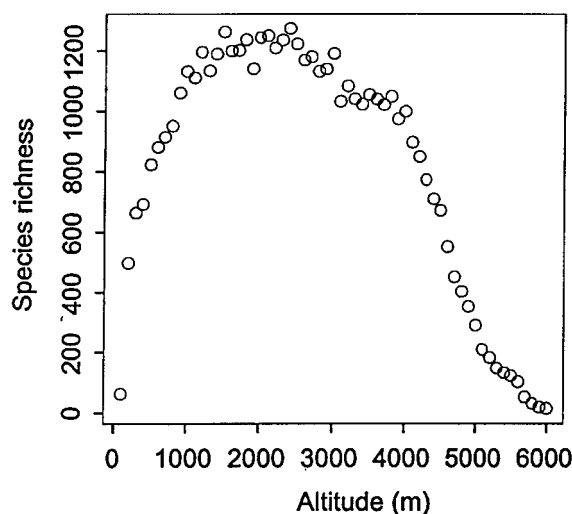


Figure 2: The observed species richness pattern along altitude in the Nepalese Himalayas.

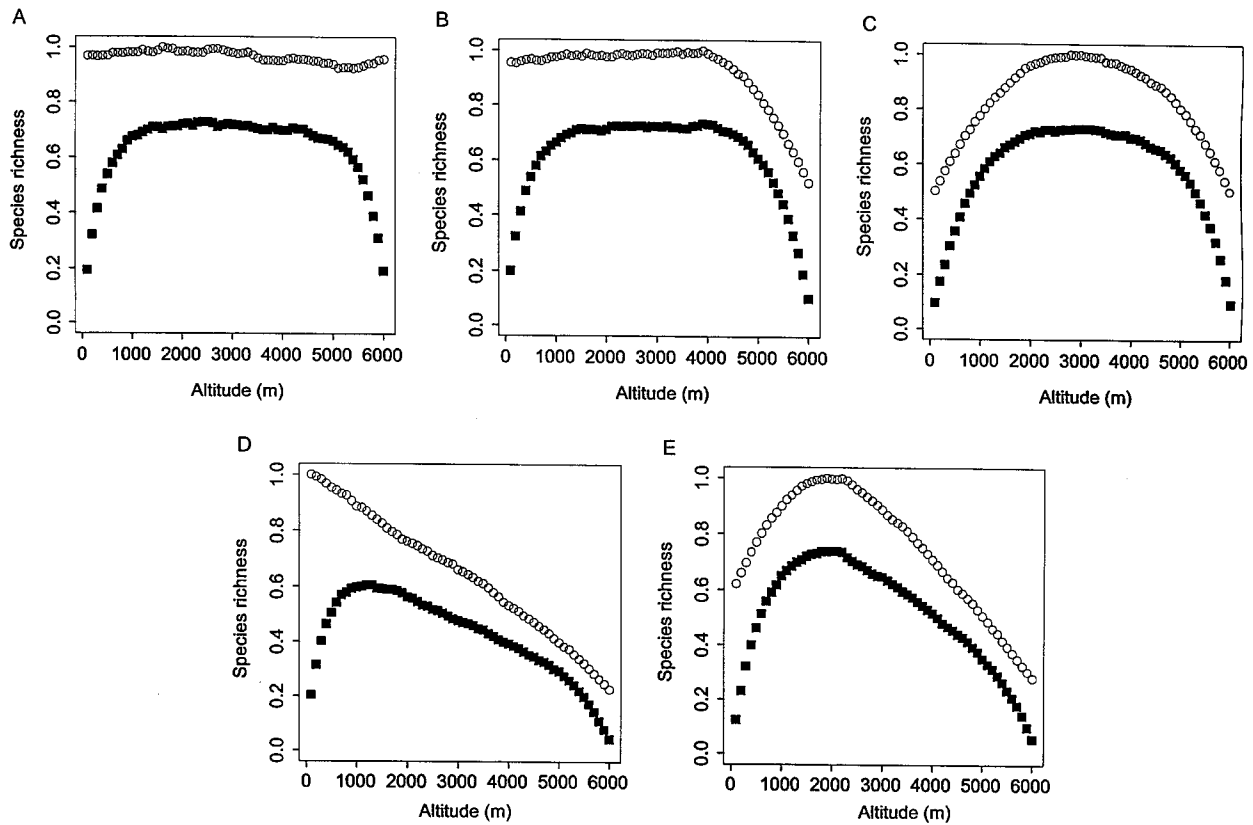
496 species), probably because the total area of these low altitudes in Nepal is very small.

#### *Model 0*

The simulated actual species richness using Model 0 shows no trend along the altitude gradient (fig. 3A). Simulated incomplete sampling and new interpolation cause a drastic decrease in richness at the extreme ends of the gradient (fig. 3A). In the interval between approximately 1,000 and 5,000 m a.s.l., there is no trend in simulated sampled species richness (fig. 3A), but it is reduced to approximately 70% of the simulated actual species richness. At the very extreme ends, this is reduced further to 20%; that is, species richness consists of only the species sampled. If the simulations allow more complete sampling, the altitudinal interval with no trend increases, and it decreases if a lower proportion of species sampled is assumed (results not shown).

#### *Models I and II: Hard Boundaries*

Simulating a hard upper boundary results in a decrease in the simulated actual species richness from 4,000 m a.s.l. and toward the top (fig. 3B). Simulated incomplete sampling and new interpolation result in a slightly asymmetrical curve (fig. 3B). The species richness pattern at lower altitudes is similar to the pattern under Model 0 (fig. 3A), whereas at the upper end the decrease in species richness is less steep in the model with the upper boundary. Simulating two hard boundaries provides a symmetric curve for simulated actual species richness (fig. 3C). Incomplete sampling and new



**Figure 3:** The simulated species richness pattern along altitude. Open circles describe the pattern with complete sampling assumed (i.e., simulated actual species richness). Filled squares describe the pattern when the probability of sampling a species where it is present is assumed to be 20%, and new observed ranges are interpolated between the maximum and minimum of the sampled species presences (i.e., simulated sampled species richness). Different subfigures represent different assumptions. *A*, No hard boundaries (Model 0). *B*, Only upper hard boundary (Model I). *C*, Both upper and lower hard boundaries (Model II). *D*, Upper hard boundary in addition to a linear underlying trend in species richness (Model III). *E*, Both upper and lower boundaries in addition to a linear underlying trend in species richness (Model IV). See text for further description of the null models. Species richness of 1.0 corresponds to maximum species richness for each model.

interpolation result in a pattern where maximum species richness is found in a smaller altitudinal range than for Model 0 (i.e., between 1,800 and 4,200 m; fig. 3C).

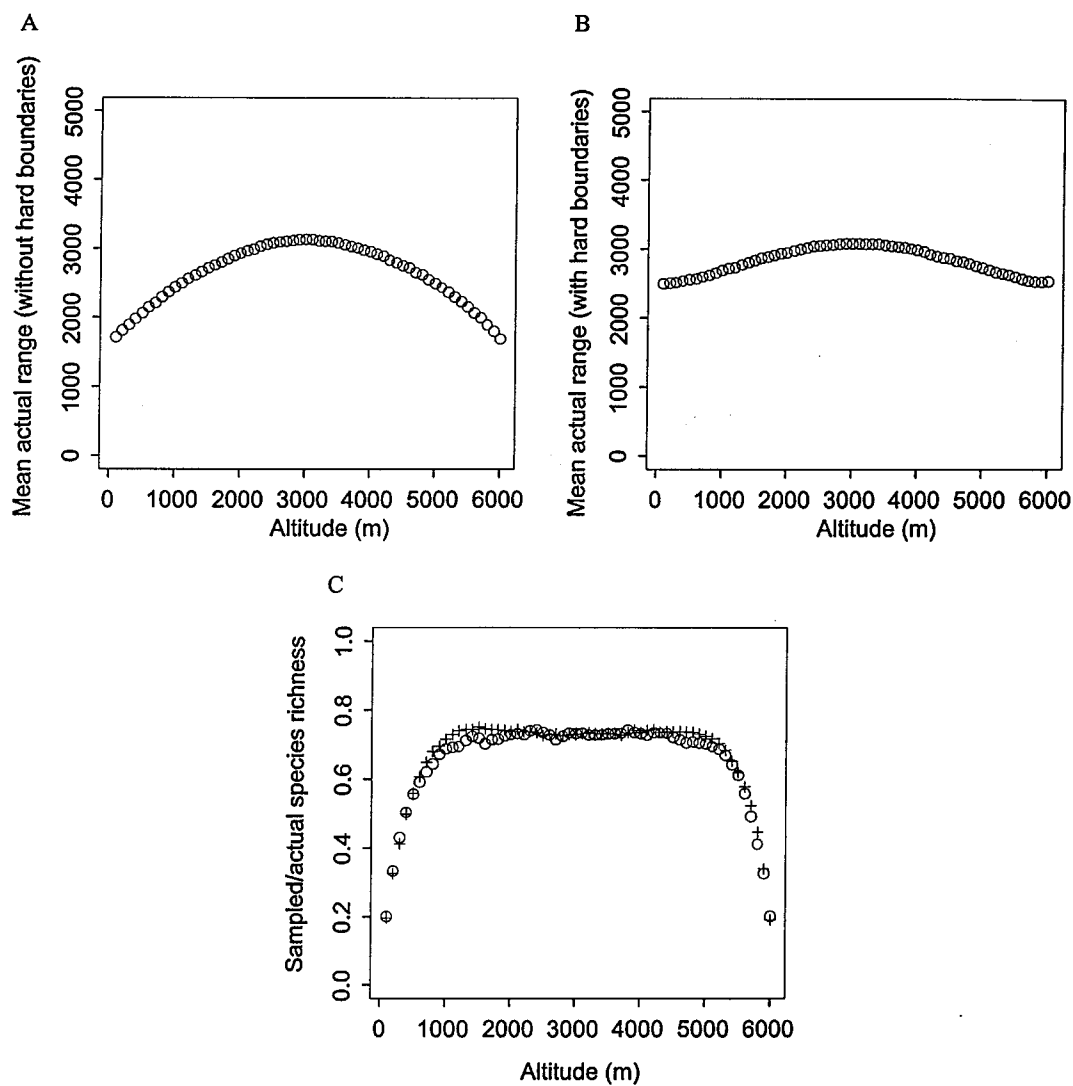
#### Models III and IV: Linear Trend

Simulating an underlying decreasing trend in species richness with increasing altitude including an upper hard boundary gives a monotonically decreasing trend from low to high altitudes (fig. 3D). The simulated effect of incomplete sampling results in a severely skewed unimodal species richness pattern (fig. 3D). Maximum species richness is now a well-defined peak at approximately 1,000 m a.s.l. Assuming two hard boundaries together with an underlying linear trend results in an asymmetrical unimodal curve that reaches its maximum between approximately 1,500 and 2,200 m a.s.l. (fig. 3E). The simulation of in-

complete sampling results in a similar curve, but the decrease toward the gradient boundaries is significantly enhanced (fig. 3E).

#### Interactions between Hard Boundaries and Interpolation Method

Plots of mean range sizes of species found for each altitude band (called "Stevens plot" by Rohde et al. [1993]) for Model 0 and Model II are shown in figure 4A and 4B. For the model with hard boundaries (Model II), mean species ranges vary from 2,500 m at the lowest and highest altitudes to 3,000 m in the middle of the altitudinal gradient. The actual ranges resulting from the no-hard-boundaries model (Model 0) show a steeper decrease in range size toward the altitudinal extremes as expected. Even though there are clear differences in the range-size patterns be-



**Figure 4:** Stevens plot (mean range size for all species found in a certain 100-m altitude band) for the actual range sizes resulting from Model 0 (A) and Model II (B). Model 0 gives smaller ranges toward the extreme altitudes because the optima are allowed to lie outside the focal domain. C, There is no visible difference in the fraction of sampled species richness versus actual species richness for Model 0 (circles) and Model II (plus signs).

tween the two models, the ratio of simulated sampled species richness to simulated actual species richness is the same for the two (fig. 4C). This indicates that interpolation does not interact with the effect of smaller or larger ranges toward the ends.

#### Discussion

Comparison between the simulated patterns (fig. 3) and the observed pattern (fig. 2) shows that figure 3E with

incomplete sampling resembles the observed pattern best. This suggests that the observed species richness is influenced by a combination of hard boundaries, an underlying decreasing trend in species richness with altitude, and incomplete sampling combined with interpolation. However, the simulation results do not precisely fit the observed pattern, which suggests that other factors may be involved or that the parameters for the factors used here are not completely correct. We will discuss incomplete sampling and interpolation, hard boundaries, an underlying linear

trend, and the influence these have on the species richness pattern in more detail, starting with species interpolation.

### *Sampling and Interpolation*

Earlier works have emphasized that an equal sampling effort may result in sampling unequal proportions of the total species richness, which may affect the altitudinal species richness patterns (McCoy 1990; Colwell and Hurtt 1994). We show that sampling an equal proportion (20%) of the species actually present in an altitudinal band may create an artificial decrease in species richness toward the boundaries when interpolation is used (fig. 3A). The reason for this decrease is that richness toward the boundaries consists only of observed species, whereas at other altitudes, richness consists of observed species plus the species added by interpolation. Interpolation has been used in many studies to correct for possible sampling problems and is perhaps the only reasonable approach when data from regional surveys are used (Williams et al. 1996; Lees et al. 1999). It is therefore important to acknowledge that this will create an artificial pattern. It is difficult to account exactly for the artifact caused by interpolation because we will never know the proportion of the total amount of species actually sampled. Further complications may arise if we say that the proportions may vary along the gradient, for example, if the proportions are dependent on species richness as suggested by Colwell and Hurtt (1994). However, by making a null model with incomplete sampling, we may be able to say something about where interpolation affects the species richness pattern. Even if we here assume a quite low proportion of species sampled (20%), the effect is nevertheless restricted to the edges of the total gradient (approximately 1,000 m from the extremes; fig. 3A).

Several studies that interpolate species presence between extreme altitudes find the highest species richness at mid-altitudes (e.g., Stevens 1992; Rahbek 1997; Fleishman et al. 1998; Nathan and Werner 1999). However, possible artifacts due to interpolation are not discussed in such studies. The same problem as described here for altitudinal gradients will also appear when latitudinal patterns in species richness are investigated by interpolation. For species richness patterns based on interpolated maps (e.g., most available distribution maps), the pattern may be more or less affected by this problem depending on how much of the distributions are interpolated.

For some conspicuous groups, for example, *Rhododendron* (Noshiro 1997; Vetaas 2000), a more complete knowledge of the altitudinal distribution of these species in Nepal can be assumed. However, it is likely that the species are actually not present in all altitudinal bands between the extremes (due to, for example, a lack of suitable habitats or competitive exclusion), so species richness will still tend

to be overestimated in midaltitude bands compared with the bands at the extremes of the gradient. Therefore, an artificial humped relationship may emerge when interpolation is used even when a complete sampling is achieved.

### *Hard Boundaries*

Apart from sampling artifacts and correlations with the environment, hard boundaries have been emphasized as an important factor in the humped relationship between species richness and altitude (Colwell and Hurtt 1994; Rahbek 1997; Colwell and Lees 2000). Even though the simulation procedure used here differs somewhat from previous studies, the effect of hard boundaries in our approach also gives maximum species richness at midaltitudes (Colwell and Hurtt 1994; Pineda and Caswell 1998). However, in our models, the species richness close to the hard boundaries decreases less than in previous models, where species richness goes toward zero as the boundaries are approached. In our models, the species richness at the extremes will be made up of all the species that have their potential ranges cut off as they meet the hard boundary. These are the species that will stack up along the borders of the triangles defined by the scatterplot of actual range versus actual midpoint in figure 1A in Colwell and Lees (2000). This stacking will be more evident if a complete sampling is assumed than with incomplete sampling. The species richness found by interpolation and incomplete sampling decreases steeply toward the extremes, which makes it resemble previous simulated patterns. The cause of this steep decrease is related to interpolation and incomplete sampling in our models, which is different from the models of Colwell and Lees (2000).

In this study, we also try to separate the effect of hard boundaries from the effects that incomplete sampling and interpolation have on species richness. We demonstrate that hard boundaries alone give a symmetrical humped relationship between species richness and altitude (fig. 3C). This means that a humped species richness curve will be observed independent of whether sampling is complete and whether interpolation is used as long as hard boundaries are present. The inclusion of hard boundaries in the simulations affects the range sizes toward the ends of the altitude gradient. We suspected that this, in turn, could influence how the effect of interpolation is interpreted. However, the observed relative difference in mean actual ranges for Model 0 and Model II had little impact on the effect of interpolation (fig. 4).

The exact shape of the humped curve depends on the maximum range allowed and the frequency distribution of range sizes (see Colwell and Hurtt 1994). Hard boundaries will have a larger effect toward midaltitudes if we allow for a larger maximum range. Theoretically, hard



boundaries will influence species richness 2,500 m from each boundary when a maximum range is 5,000 m, as is used here.

Hard boundaries are usually used to refer to any barrier for dispersal into the study area (Colwell and Hurtt 1994; Colwell and Lees 2000). Another possible interpretation is that mass effect (Shmida and Wilson 1985) or source sink dynamics (Pulliam 1988) are relatively more important within an altitudinal gradient than along a latitudinal gradient. The short horizontal distances along an altitudinal gradient may give the opportunity for species to colonize in areas where local population growth is negative without continuous input from more optimal areas (Shmida and Wilson 1985; Pulliam 1988), whereas the large distances along latitudinal gradients prevent species with ecological optima below sea level, or in climatically more favorable areas, from having a large influence on the studied altitudinal gradient. In practice, this means that areas in the midaltitudes receive input from two directions, whereas areas close to the gradient ends receive input from one direction only.

#### *Underlying Linear Trends and Correlations with Environment*

The effects of hard boundaries and interpolation both result in a symmetric hump in species richness along altitude. The observed species richness curve clearly shows that species richness reaches a maximum at the lower end of the altitudinal gradient (fig. 2). The asymmetric hump has also been noted by other authors (Rahbek 1997; Fleishman et al. 1998). Simulations performed in this study demonstrate that an underlying linearly decreasing trend with altitude will, in combination with hard boundaries and/or interpolation, give an asymmetric hump in species richness along altitude. This underlying trend is the effect that the environment has on the number of species if we say that hard boundaries are a nonenvironmental effect. This suggests that we have to search for factors that are linearly or at least monotonically decreasing or increasing with altitude to explain the relationship between species richness and the environment. The formula for the linear trend used here is clearly not catching all the variation in the observed species richness. We could probably get a simulated species richness curve to mimic the observed species richness more closely by changing the parameters in the different simulations. However, this would give the false impression that we imply that the observed species richness is determined only by the factors (with the parameters given) we have included. This is not the case. We only want to emphasize that the broad pattern (a skewed unimodal species richness curve) can be explained

by a combination of the presence of hard boundaries, interpolation, and environmental factors that probably have a monotonic trend with altitude.

One popular explanation for the decrease in species richness with latitude is the decrease in productivity from the equator toward the poles (Rohde 1992). This has also been used to explain the patterns in species richness when a monotonic decrease in species richness with altitude is found (Rahbek 1997 and references therein). Singh et al. (1994) found that productivity in the Indian Himalayas does not change between sea level and approximately 2,500 m. Only above this altitude does it start to decrease. However, several other plausible explanations have been given for a linear relationship between species richness and altitude (e.g., Givnish 1999), and to differentiate between the different possibilities requires more detailed knowledge about both the species richness pattern and the variation of environmental factors with altitude in the Nepalese Himalayas.

It is impossible to say whether most or all of the humped relationships between species richness and altitude are a result of an underlying monotonic trend with the environment because it is not possible in most cases to evaluate the importance of hard boundaries. We do, however, know that hard boundaries affect the species richness pattern, but we do not know exactly how they affect it. We therefore need more information on how hard boundaries influence species richness so that we can take account of this and then seek correlations between richness and the environment.

#### *Conclusions*

All three factors evaluated in this study have an effect on the observed pattern in species richness. The complexity of each factor makes it impossible to evaluate the relative importance or the exact shape for which each factor is responsible. Hard boundaries and an underlying linear trend yield a species richness pattern similar to that observed, but the steep decrease in richness toward the gradient boundaries is obtained only by additional assumptions, namely, incomplete sampling and subsequent interpolation. The location and the interval of maximum species richness correspond better to the observed pattern in species richness when two hard boundaries are assumed, compared with one or no hard boundary. We therefore propose that all factors (hard boundaries, underlying monotonic trend in species richness, incomplete sampling and interpolation) in combination may be responsible for the observed pattern in species richness along the altitudinal gradient in the Nepalese Himalayas.

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