

## LETTERS

# Scale effects and human impact on the elevational species richness gradients

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Despite two centuries of effort in characterizing environmental gradients of species richness in search of universal patterns, surprisingly few of these patterns have been widely acknowledged<sup>1–3</sup>. Species richness along altitudinal gradients was previously assumed to increase universally from cool highlands to warm lowlands, mirroring the latitudinal increase in species richness from cool to warm latitudes<sup>1,4,5</sup>. However, since the more recent general acceptance of altitudinal gradients as model templates for testing hypotheses behind large-scale patterns of diversity<sup>5–9</sup>, these gradients have been used in support of all the main diversity hypotheses, although little consensus has been achieved. Here we show that when resampling a data set comprising 400,000 records for 3,046 Pyrenean floristic species at different scales of analysis (achieved by varying grain size and the extent of the gradients sampled), the derived species richness pattern changed progressively from hump-shaped to a monotonic pattern as the scale of extent diminished. Scale effects alone gave rise to as many conflicting patterns of species richness as had previously been reported in the literature, and scale effects lent significantly different statistical support to competing diversity hypotheses. Effects of scale on current studies may be affected by human activities, because montane ecosystems and human activities are intimately connected<sup>10</sup>. This interdependence has led to a global reduction in natural lowland habitats, hampering our ability to detect universal patterns and impeding the search for universal diversity gradients to discover the mechanisms determining the distribution of biological diversity on Earth.

Studies of altitudinal gradients in species richness have increasingly replaced the latitudinal gradient as a model template for large-scale gradient studies<sup>9</sup>. Altitudinal gradients encompass several gradients in climatic and environmental factors, such as area, net primary productivity and geometric constraints. These factors are expected to influence spatial variation in species richness (Supplementary Fig. 1) but are often correlated, making hypothesis testing problematic and controversial<sup>3</sup>. However, these very controversies make altitudinal gradients an illuminating field of study. A recent quantitative analysis of altitudinal species richness gradients including 204 data sets demonstrated that about 50% of the pattern distributions were hump-shaped, about 25% showed a monotonically decreasing pattern, and about 25% followed other distributions<sup>9</sup>. It has therefore been suggested that non-generality in altitudinal species richness patterns may be a result of differences in spatial design between studies<sup>9</sup>. These differences include the choice of grain size and the extent and proportion of gradients sampled. Nevertheless, statistical correlations between these diverse patterns and associated patterns of climate<sup>11,12</sup>, area<sup>8,13,14</sup> and, more recently, geometric constraints<sup>8,15</sup> have been used as support for competing hypotheses<sup>5,9,13,16,17</sup>.

In this study we used an extensive data set comprising 400,000 records covering 3,046 species of vascular plants, lichens and bryophytes from the Pyrenees to illustrate and evaluate the sensitivity of patterns to scale effects (see Methods). Scale effects were evaluated by re-sampling the data set and generating altitudinal species richness patterns after changes in grain size (that is, the resolution at which data are sampled) and the scale of extent (that is, the proportion of the complete altitudinal gradient sampled). In association with scale of extent, we also evaluated the effect of omitting segments from the lowest or highest ends of the gradient.

The relationship between species richness and altitude varied greatly with scale of extent (Fig. 1). When the entire elevational gradient was surveyed, the pattern was hump-shaped (top row in Fig. 1), changing progressively to a monotonically decreasing pattern as the scale of extent diminished. This trend was particularly apparent when the lower limit of the gradient was excluded from the analyses. When the upper limit of the gradient was excluded, the hump-shaped pattern was less sensitive to changes, although a monotonic increase in richness with altitude ultimately became apparent (Supplementary Fig. 2). This pattern has previously, although infrequently, been reported<sup>5,9</sup>. Regardless of which gradient segment was omitted, grain size did not markedly affect changes in species richness with elevation (Fig. 1 and Supplementary Fig. 2). This 'negative' result is noteworthy because variation in grain size has previously been shown to significantly influence the relative importance of factors determining large-scale continental patterns of species richness<sup>18</sup>.

The implications of these scale effects for the assessment of competing diversity hypotheses were evaluated statistically. The empirical data on species richness were compared with predicted data generated by four well-documented diversity models developed to explain altitudinal and environmental species richness gradients<sup>15</sup>. Model 1 is a monotonic species-richness–productivity model in which productivity and, consequently, species richness are assumed to decrease with altitude; model 2 is a monotonic species-richness–area model in which area and, consequently, species richness are assumed to decrease with altitude; model 3 is a hump-shaped species richness–productivity model in which productivity is assumed to decrease with altitude and species richness is assumed to peak within the lower half of the gradient; and model 4 is a mid-domain-effect model with a peak in richness in the middle of the gradient as a consequence of geometric constraints and two hard boundaries. Because the four models are based on generalized functions, it is possible to choose the function that suits any specific pattern relevant to a given data set; for example, if most of the area occurs at mid-altitude regions, model 3 or 4 will be better suited to illustrate how scale effects may influence the interpretation of empirical analyses (see Methods for details, and Supplementary Fig. 1 for additional details on the four models).

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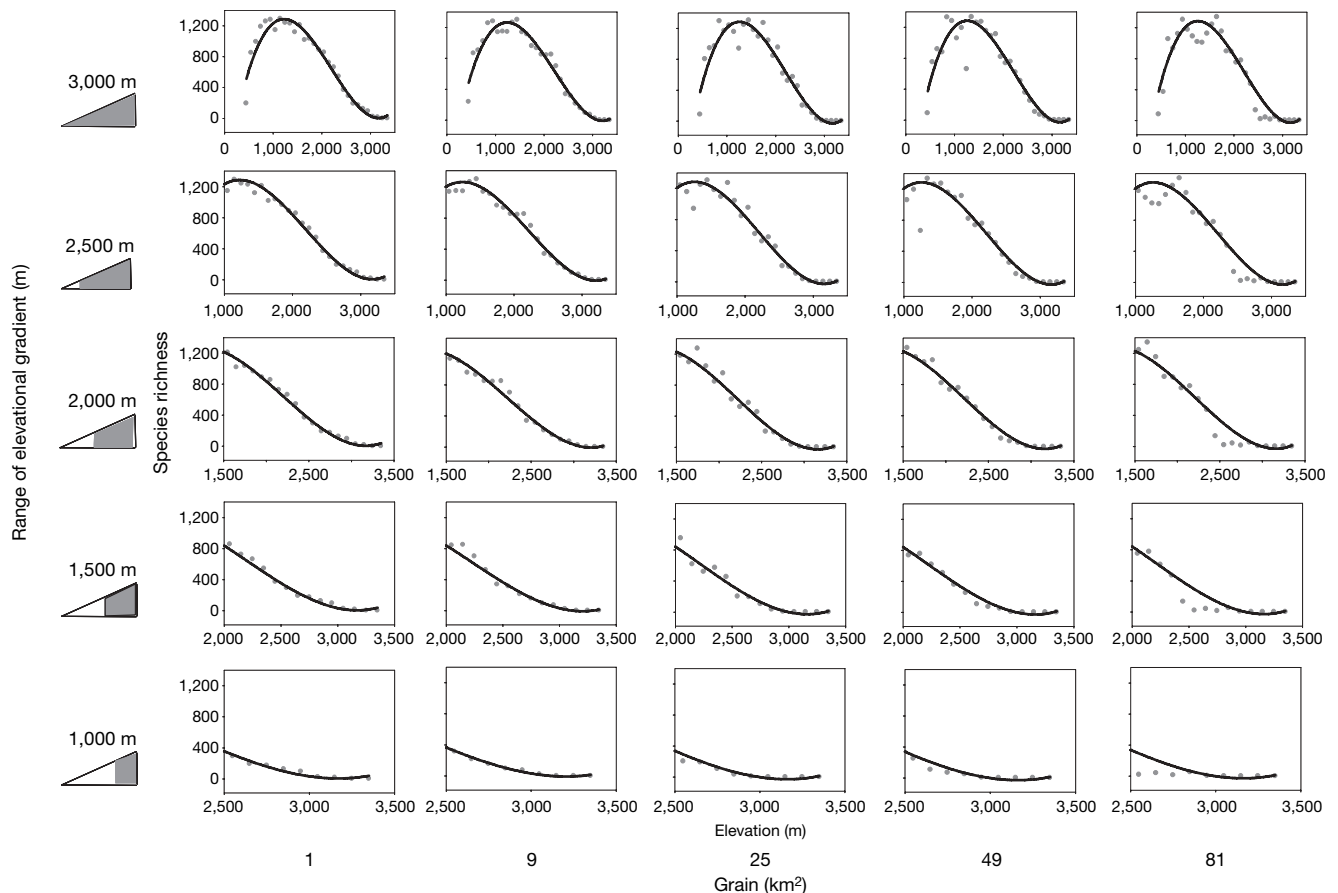
As expected, the correlation was best between the empirical hump-shaped pattern for the entire gradient and the predictions from models 3 and 4 (Fig. 2). However, when the extent of scale was reduced to cover a smaller segment of the gradient, models 1 and 2 provided a better correlation, especially when the lower limit of the gradient was omitted (Fig. 2B, a). Thus, statistical evidence supporting the hump-shaped models 3 and 4 increases when a larger proportion of the gradient is included. Goodness-of-fit values within each of the four diversity models also varied depending on whether gradient segments from the lower or upper limits were omitted (Fig. 2). In contrast, all correlation patterns were consistent across different grain sizes.

Scale effects have previously been quantified for the productivity–diversity gradient<sup>19</sup>. It has long been recognized that truncation of a gradient may affect species richness patterns<sup>20</sup>, whereas tabulation of the shape of the pattern of altitudinal species richness has suggested that these may be sensitive to scale effects<sup>9</sup>. Until now, with the use of altitudinal gradient data to test hypotheses related to species diversity, the quantitative and qualitative impacts of scale effects and their consequences have never been explicitly assessed, and as a consequence of this the effects of scale have generally been underestimated. Previous studies acknowledging potential scale issues have attempted to circumvent these effects by, for example, considering only studies that have sampled in excess of 70% of the gradient<sup>21</sup>. However, as we show here, even the smallest truncation of the gradient can completely shift the statistical support for competing hypotheses. This degree of sensitivity to scale effects may well be universal<sup>22</sup>, as we obtain the same results when repeating our analyses with a data set from Costa Rica<sup>23</sup>, which is one of the very few

complete single-transect, tropical elevational gradients remaining in the world (see Supplementary Fig. 3).

It is difficult to compare altitudinal studies or to use explicit meta-analysis statistics because studies are conducted on various organisms and in all parts of the world, with each evaluation requiring the use of case-specific study designs. In addition, almost all gradients have a unique history of human intervention in the environment. The variables characterizing the organisms, their environment and their perception of scale are intercorrelated<sup>9</sup>, and the absence of suitable factorial techniques<sup>24</sup> makes the meta-analysis of potential scale effects difficult to interpret. Following the approach described in this paper—that is, resampling the same empirical data at various scales of analysis<sup>18</sup> and subsequently exploring the statistical relationships between empirical and predicted patterns conditional on competing diversity hypotheses—can circumvent some of these problems and seems to be a powerful technique.

On the basis of a few studies, the altitudinal species richness pattern was previously considered to be universal, with monotonic declines in richness with increasing altitude (and, it was believed, with decreasing temperature and resources)<sup>1,4,5</sup>. Today, with more than 1,000 studies<sup>9</sup>, the altitudinal pattern is seen to be more complex. However, monotonic declines and hump-shaped patterns with peak richness at a wide range of altitudes are the most commonly reported patterns<sup>5–9,11,13,16,17</sup>. The perception of varying altitudinal patterns and the current lack of consensus on the mechanisms controlling altitudinal variation may be due largely to scale effects. Differences in sampling regimens, study quality and the sheer magnitude and diversity of studies may also contribute to the wide variability in patterns.



**Figure 1 | Scale effects on altitudinal species richness patterns.** These bivariate plots, generated by repeated sampling of the same data set, show the empirical species richness patterns based on 25 combinations of scale of extent (y axis) and grain size (x axis). The surveyed gradient was reduced by

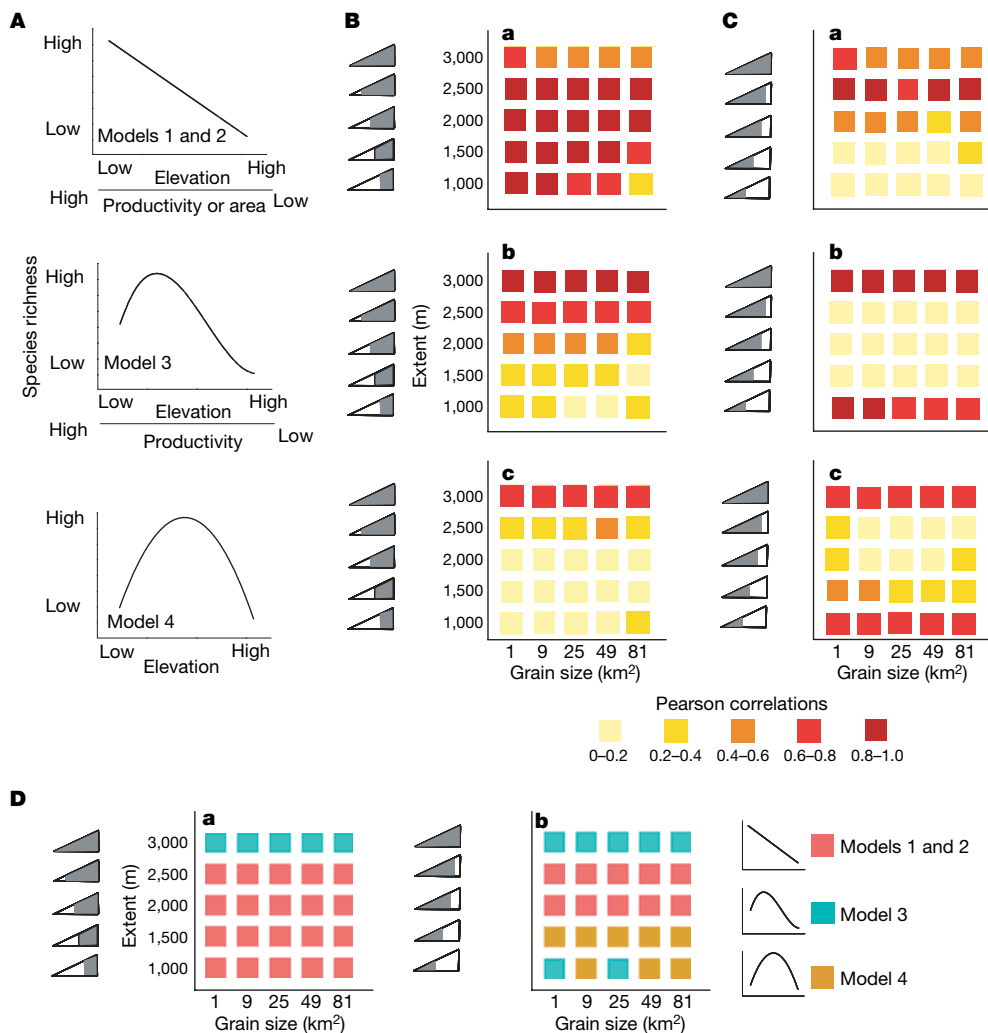
omitting segments from the lower limit. The sampled gradients are illustrated by the grey shaded areas in the triangles adjacent to the y axes. (Supplementary Fig. 2 shows the effects of scale as a result of omitting segments from the upper limit of the gradient.)

The results presented here do not provide direct evidence that a hump-shaped altitudinal species richness pattern describes the universal distribution better than a monotonically decreasing pattern. However, the results indicate that the extent of scale and omission of a part of the gradient tend to favour the monotonic pattern (see also Fig. 2 in ref. 9). In particular, the omission of the lowest part of the gradient produces a monotonic pattern (Fig. 2). A uniform pattern of human impact on altitudinal gradients worldwide (see below) may cause this scale effect to become a unidirectional bias.

In mountainous areas, lower regions are affected by settlements and exploitation of forest resources, and zones above the tree line are subject to grazing and anthropogenic fire practices intended to maintain grassland and to lower the tree line. Accordingly, deforestation is generally most extensive in the lowlands and at high altitudes, with most forest remaining at mid-altitude (Fig. 3a), while overall human impact is larger in the lowlands and decreases almost monotonically with increased elevation (Fig. 3b). That is, human activities have generally affected worldwide the lower and upper slopes more than the mid-altitudinal habitats (Fig. 3 and Methods). Today, it is increasingly rare to localize and work on complete, natural and untouched altitudinal gradients ranging from

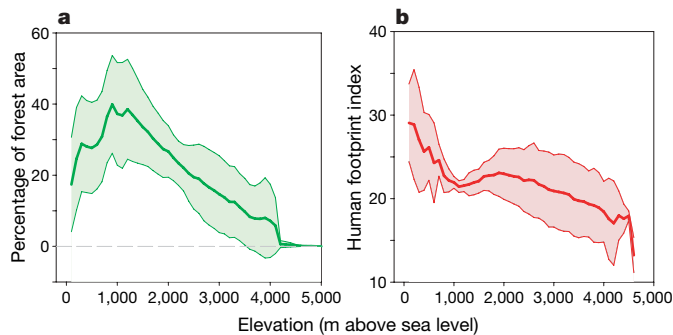
sea level to high-altitude mountaintops. Most of the existing 461 studies (Methods) have been conducted on gradients that include disturbed lowlands<sup>5</sup>. All regional studies include disturbed areas, and out of 203 single-transect altitudinal studies only 12 have been conducted on complete and natural gradients (Supplementary Tables 1 and 2). Paradoxically, the alternative solution of excluding lowland zones from analysis if the natural habitat has been destroyed—that is, the inclusion of lowland habitats even if disturbed—can also cause a bias towards a monotonic pattern. Disturbed habitats often have an elevated level of species richness as a result of the invasion of habitat generalists, which more than compensates for the potential loss of habitat specialists<sup>25</sup>.

To manage biodiversity, today and in the future, it is crucial to understand the processes behind the observed natural patterns of biodiversity<sup>26</sup>. Unfortunately, because humans have destroyed many of the natural patterns it may be difficult to discover the mechanisms determining these patterns and to generate the knowledge required to manage biodiversity and natural systems efficiently and wisely. It is possible that human impact may already have permanently affected our ability to detect the processes that engender patterns of diversity.



**Figure 2 | Scale effects on patterns of altitudinal species richness and testing of four generalized diversity models.** **A**, Schematic illustration of expected species richness patterns for four diversity models (see the text, Methods and Supplementary Fig. 1 for additional details on models). **B**, Degree of correlation (Pearson) between expected and empirical species richness values in 100-m altitudinal zones when sampling the same data with different combinations of grain size (1, 9, 26, 48 and 81 km<sup>2</sup>) and scale of extent (omitting segments of 0, 500, 1,000, 1,500 and 2,000 m from the lower

limit of the gradient as illustrated by the grey-shaded area of the small triangles next to each of the y axes). **a**, Models 1 and 2; **b**, model 3; **c**, model 4. **C**, As in **B**, but omitting segments from the upper limit of the gradient. **D**, Coloured squares indicate the model with the highest Pearson correlation (that is, the best fit) for 25 combinations of grain size and spatial extent when omitting segments from the lower (**B**) and upper (**C**) limits of the gradient, respectively, from the analysis.



**Figure 3 | Worldwide and generalized pattern of human impact along the altitudinal gradient.** **a**, The bold green line indicates the percentage of area covered by forest (natural vegetation). **b**, The bold red line indicates the averaged human footprint index for each elevational band of 100 m above sea level. The lines are averaged on the basis of data from 13 of the largest mountain regions in the world. Shaded coloured areas indicate  $\pm 0.5$  s.d. boundaries of the averaged values (for calculations see Methods, and see Supplementary Figs 4–6 for location and data for the 13 individual mountain regions).

### METHODS SUMMARY

Scale effects were illustrated by using an empirical data set based on 400,000 site–species records of vascular plants, lichens and bryophytes<sup>27</sup> from the central Spanish Pyrenees (13,500 km<sup>2</sup>) covering a complete regional altitudinal gradient, from the bottom of the valley at 400 m above sea level to 3,100 m above sea level. For the purpose of this paper it was assumed that the empirical data were without sampling errors or biases, and the derived altitudinal patterns of species richness were accepted at face value. Thus, no conclusions with regard to factors determining the Pyrenean altitudinal pattern of species richness should be derived from these analyses.

Species richness was calculated for each 100-m altitudinal band by using the Idrisi GIS software<sup>28</sup>, varying grain size and scale of extent (Fig. 1 and Supplementary Fig. 2). Evaluations of scale effects on patterns of species richness and on the correlative fit between empirical and predicted data were done by resampling the distributions of 3,046 species. This was performed with five grain sizes (1, 9, 25, 49 and 81-km<sup>2</sup> cells) in combination with five scales of extent, for a total of 25 sampling combinations. Reduction in scale of extent was achieved through the omission of segments of 0, 500, 1,000, 1,500 and 2,000 m from the lower and upper limits of the original gradient.

The expected altitudinal pattern of species richness was calculated for four main diversity models of altitudinal variation in species richness (Methods and Supplementary Fig. 1). Predicted values of species richness were correlated with the empirical data for each altitudinal band by using the Pearson product moment correlation (see Methods for details). This was done for the 25 combinations of scale of extent and grain size for each of the four models (Figs 1 and 2, and Supplementary Fig. 2).

**Full Methods** and any associated references are available in the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

**Received 26 December 2007; accepted 4 February 2008.**

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

**Acknowledgements** We thank J. Hortal, F. W. Larsen, and D. Alagador for comments on the manuscript. The research of D.N.B. (13P post-doc) was partly supported by the EC FP6 ALARM project and the DGA PM018/2006 project (Diputación General de Aragón). M.B.A., T.S.R. and C.R. acknowledge the Danish National Science Foundation for support of macroecological research; research by M.B.A. is also supported by the EC FP6 ECOCHANGE project. We thank the Pyrenean Institute of Ecology (CSIC) for providing the biological data set for the Spanish Pyrenees.

**Author Contributions** All authors designed the research. D.N.B. conducted all the analyses, except the quantitative review of the literature, which was conducted by T.R. and C.R. The manuscript was written by D.N.B. and C.R. All authors discussed the results and commented on the manuscript.

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## METHODS

**Calculation of predictive values for the four models.** The two linear diversity models (models 1 and 2; see Supplementary Fig. 1) were calculated with a linearly decreasing function constrained by the maximum and minimum values from the empirical data set. The Digital Elevation Model (DEM) within the GIS software was used to simulate a monotonic decrease in richness with altitude for each grain size and extent combination (Supplementary Fig. 7). The same procedure was used for models 3 and 4, in which the hump-shaped function was defined within the FUZZY module in the GIS software<sup>28</sup>.

**Evaluating the sensitivity of patterns to scale effects in another elevational gradient.** Here we assessed the effect of scale of extent in the Barva Transect (10° N, 84° W), a complete single-transect, tropical forested elevational gradient ranging from 40 to 2,730 m above sea level, located in the Braulio Carrillo National Park, Costa Rica, as well as adjacent areas. This transect is a unique gradient, being one of the very few complete elevational transects still existing; it has undisturbed habitats along the entire gradient while being probably the most thoroughly surveyed elevational gradients in the tropics (see <http://viceroy.eeb.uconn.edu/alas/alas.html>). The data analysed here were extracted from ref. 23. Because the data are from a single-transect gradient, we only evaluated scale effects associated with changes in the scale of extent (that is, the proportion of the complete altitudinal gradient sampled). The analyses of the correlative fit between empirical altitudinal patterns of species richness and predicted patterns of species richness were conducted for the grain size originally used in ref. 23; that is, elevational bands of 500 m (see Supplementary Fig. 3). The prediction of expected patterns followed the same method used for the Pyrenean data set (see Methods Summary); that is, for each elevational band an expected value was predicted by using the FUZZY module of the GIS software, following the functions that illustrate models 1, 2 and 3 (see Supplementary Fig. 1 for additional details on models).

**Measuring the severity of human impact along elevational gradients in global mountain regions.** The anthropogenic impacts along elevational gradients of 13 mountain ranges were evaluated (Supplementary Figs 4–6). Six of these ranges comprise tropical mountains (tropical Andes, Sierra Madre, Ethiopian highlands, Eastern Africa highlands, Mitumba mountains and Pegunungan Maoke, while seven are non-tropical (Rocky Mountains, non-tropical Andes, Pyrenees, Alps, Atlas, Caucasus and Himalayas). The Mountains of the World Geographical

Information System (GIS) database was used to delimit the boundaries of the mountain ranges (<http://www.mtnforum.org/mem/searchind.cfm?searchtype=atlas>). For each mountain range we calculated the percentage area currently covered by forest for each 100-m elevational band (an estimator of anthropogenic disturbance suggested by the authors of ref. 29 in their 'human footprint' map), by using the US Geological Survey (USGS) Global Land Cover Database (Version 2.0) as well as the USGS GTOPO30 Global Digital Elevation Model (<http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html>), both of which have a horizontal grid spacing of 30 arcsec (about 1 km). Subsequently, the 'human footprint index'<sup>29</sup>, a composite of human population and infrastructure data, was used as an estimator of human impact along the elevational gradients of the 13 mountain ranges analysed (1 km of horizontal grid spacing). We used the integrated GIS and RS (image processing) software solution, Idrisi Kilimanjaro<sup>28</sup> (Clark Labs) to measure changes in both estimators for each elevational band.

**A quantitative review of the literature assembling the reported patterns of altitudinal gradients of species richness.** The search for data sets follows the protocol of ref. 9 and is based on an ISI search performed on 12 October 2007 with the following search string: ('elevatio\*' or 'altitud\*') and ('richness' or 'diversit\*') and ('gradien\*' or 'patter\*' or 'transec\*' or 'variati\*'). The search was conducted with the option 'all document types' for the period 1990–2007 and included title, abstract and keywords. A closer examination of the more than 1,000 data sets found provided 461 data sets that contained information on the variation of species richness with altitude. Of these only 78 data sets were gradients with data points from ≤500 to ≥2,000 m above sea level (Supplementary Table 1; see Supplementary Table 2 for details on the individual studies). Of the 78 data sets, 65 gradients were completely surveyed from the valley floor to the mountaintop, and most of these were based on regional compilations. All the regional studies include mountain areas along the altitudinal gradient that are in part affected by human activities (see Supplementary Figs 4 and 5). As judged from the description in the individual papers, only 12 of the 24 complete single-transect gradient data sets (of the 461 total number of altitudinal data sets) may be based on gradients with full natural habitat along the entire gradient.

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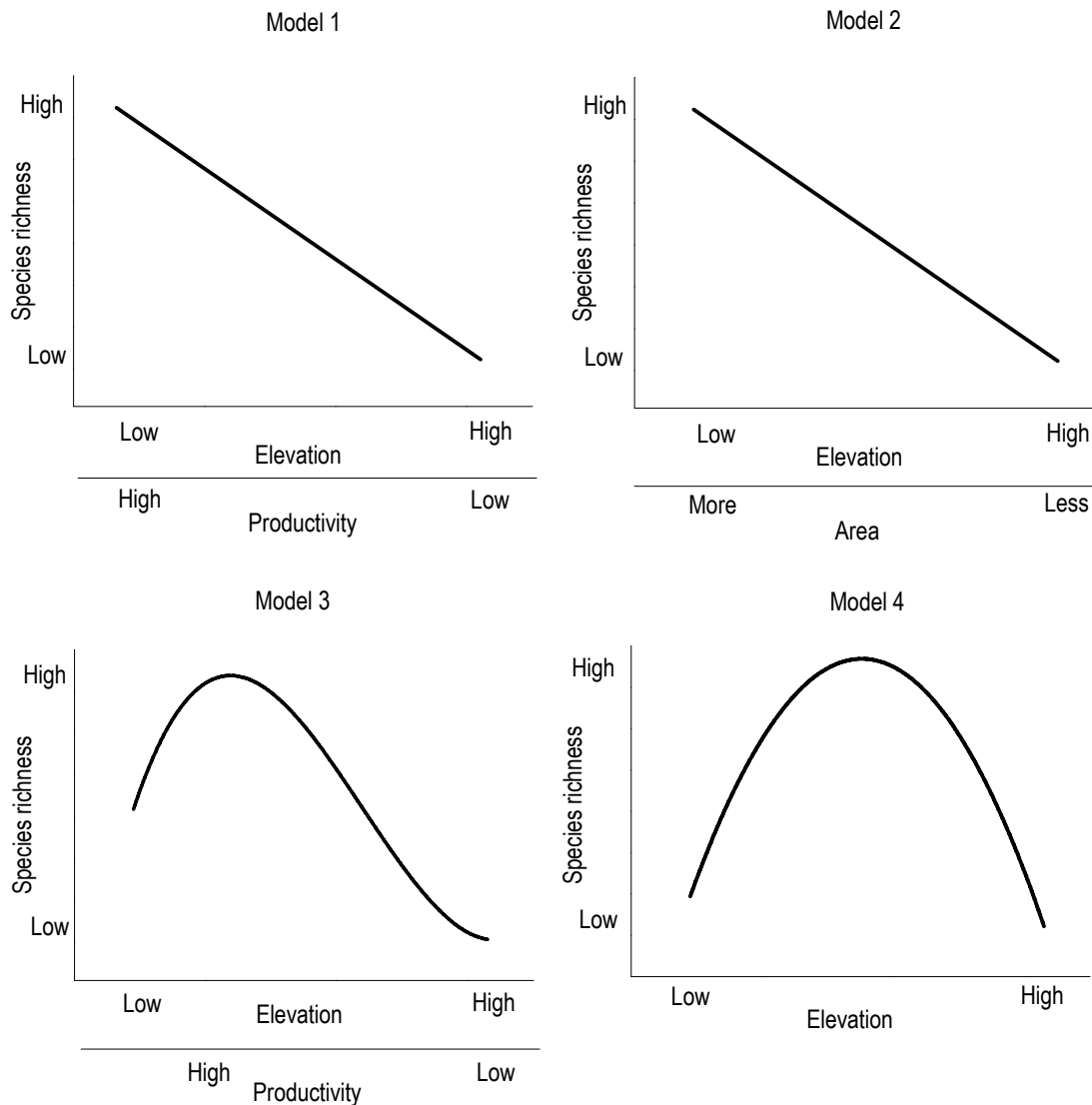
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## Supplementary Information

This file contains Supplementary Figures 1, 2, 3, 4, 5, 6 and 7, Supplementary Tables 1 and 2 and Supplementary Notes.

## Supplementary Figures



**Supplementary Figure 1.** Schematic illustration of the four main diversity models of altitudinal variation in species richness<sup>adopted and modified from 30</sup>. The four diversity models outlined in Supplementary Figure 1 present those models most commonly discussed in the literature. They focus specifically on altitudinal gradients in species richness<sup>30,31,32,33,34,35</sup>, but they also represent some of the most widely tested hypotheses regarding large-scale species richness patterns<sup>36</sup>. Therefore, these models are eminently suitable templates for the investigation of the effects of scale on species richness gradients in general, and specifically on altitudinal gradients.

Model 1, a monotonic species richness-productivity pattern, where productivity and, consequently, species richness are assumed to decrease with altitude; Model 2, a monotonic species richness-area pattern, where area and, consequently, species richness are assumed to decrease with altitude; Model 3, a hump-shaped species richness-productivity pattern, where productivity is assumed to decrease with altitude and species richness is assumed to peak within the lower half of the gradient; and Model 4, a Mid-Domain-effect model with a peak in richness in the middle of the gradient as a consequence of geometric constraints and two hard boundaries<sup>modified from 30</sup>.

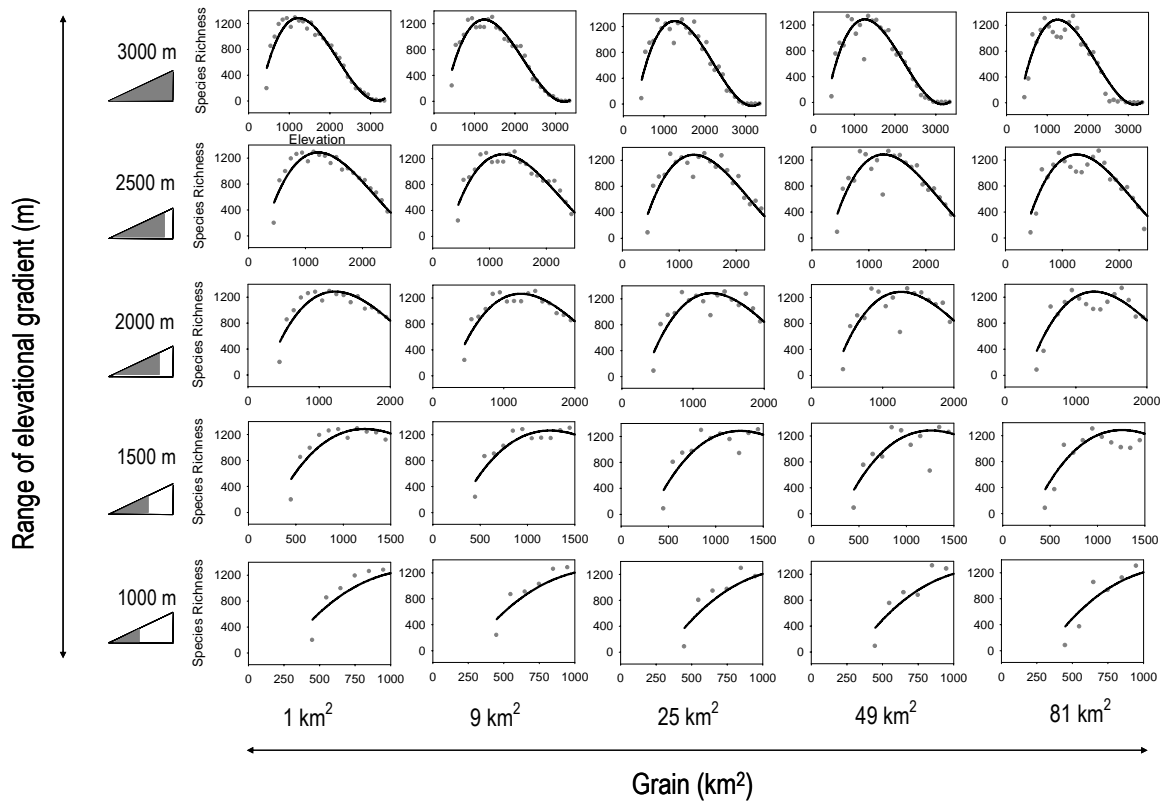
Diversity Models 1 and 3 are based on the species richness-productivity hypothesis<sup>37</sup>, which posits that solar radiation determines energy availability and productivity as well as biomass, or number of individuals. Denser populations reduce the risk of extinctions, while increasing energy leads to an increase in the number of individuals and, accordingly, in the number of species able to co-exist. Productivity (or energy) is widely believed to control species richness by setting the upper limit of contemporary carrying capacity. In this way, higher productivity can be seen to result in greater species richness. Two different models of the productivity hypothesis were used in the present study. The first model gives rise to a monotonic, positive relationship pattern between level of productivity and species richness (Diversity Model 1)<sup>37,38</sup>. The second model (Model 3) is characterized by a hump-shaped pattern, where species richness increases with productivity to a maximal level and decreases at the extreme of productivity<sup>39,40</sup>. Both models assume that productivity is highest in the lowland areas and decreases with altitude as temperature decreases. However, productivity can be higher at intermediate altitudes due to local climatic conditions. For example, many tropical forests are subject to frequent or persistent fog or clouds, which can secure atmospheric moisture through the process of 'cloud stripping' (see discussion and references in Rahbek 1997<sup>30</sup>). Thus, depending on the exact relationship between productivity and altitude, the richness patterns outlined in Models 1 and 3 could equally well support the monotonic positive or the hump-shaped species richness-productivity hypotheses<sup>30</sup>.



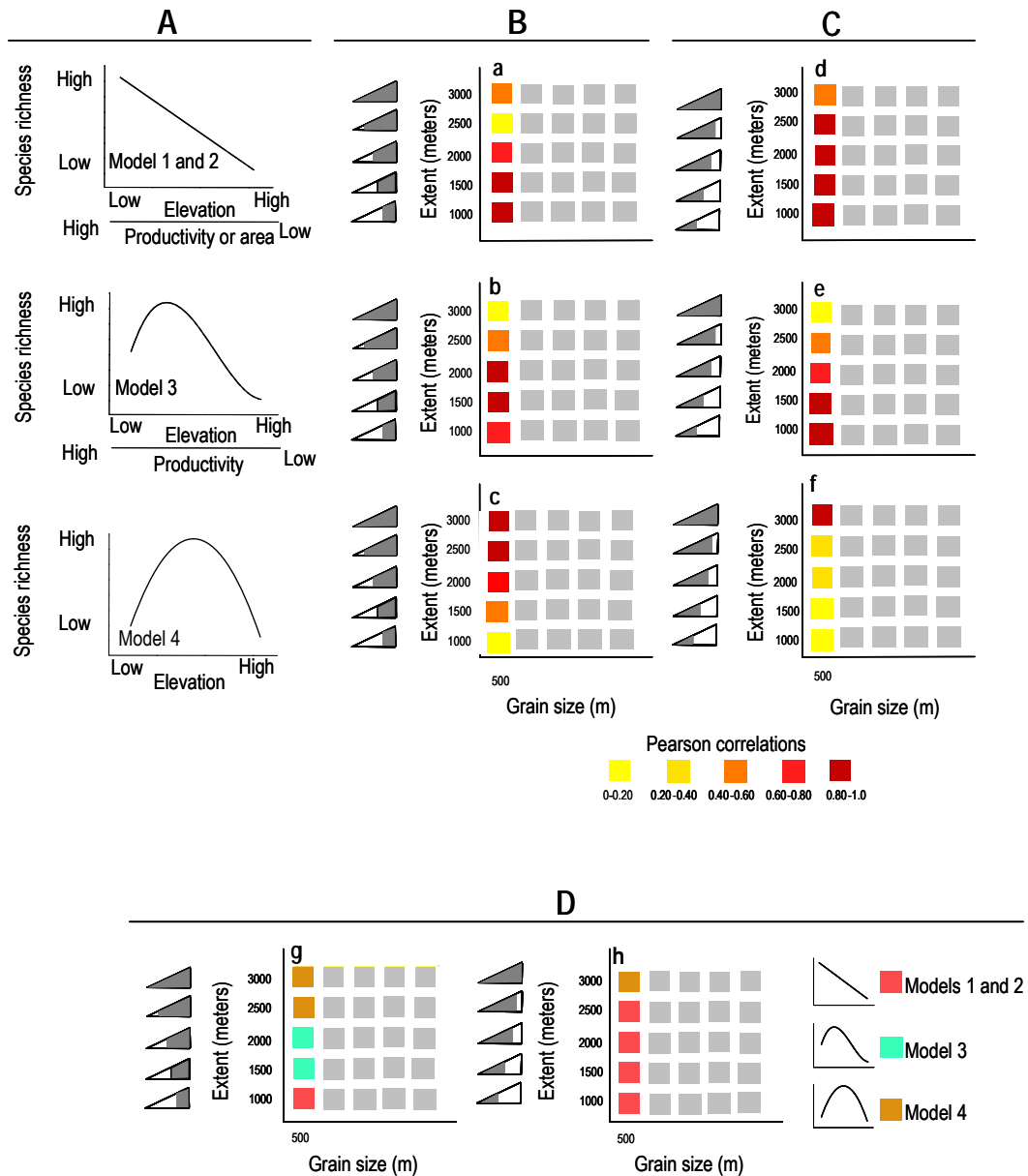
Diversity Model 2 reflects the species-area relationship, which predicts that larger areas will contain more individuals as well as a greater habitat heterogeneity (or landscape heterogeneity, depending on the scale of resolution of the analysis), and thus more species<sup>36,40</sup>. Area normally decreases with altitude in mountains<sup>41</sup>, although high-altitude plateaus frequently occur in larger mountain chains and are often larger in area per altitudinal zone than the mid-altitude zones<sup>30</sup>.

Diversity Model 4 describes the Mid-Domain effect model<sup>34</sup>, and is based on the assumption of random placement of species ranges within a domain constrained by hard boundaries. Along an altitudinal gradient, this domain would be constrained by the valley bottom and the mountain top. It predicts a peak in species richness in the middle of the altitudinal gradient.

As the four models are based on generalized functions, it is possible to choose the function that suits any specific pattern relevant to a given data set, e.g, if the majority of the area occurs at mid-altitude regions, model 3 or 4 will be better suited to illustrate how scale effects may influence the interpretation of empirical analyses. Also, other currently debated species richness diversity models can easily be placed within the constraints of the four models outlined here. For example, Rapoport's rule<sup>42</sup> and the Temperature Kinetics Model<sup>43</sup> would both predict a monotonic decline in richness with altitude similar to those described in Models 1 and 2.

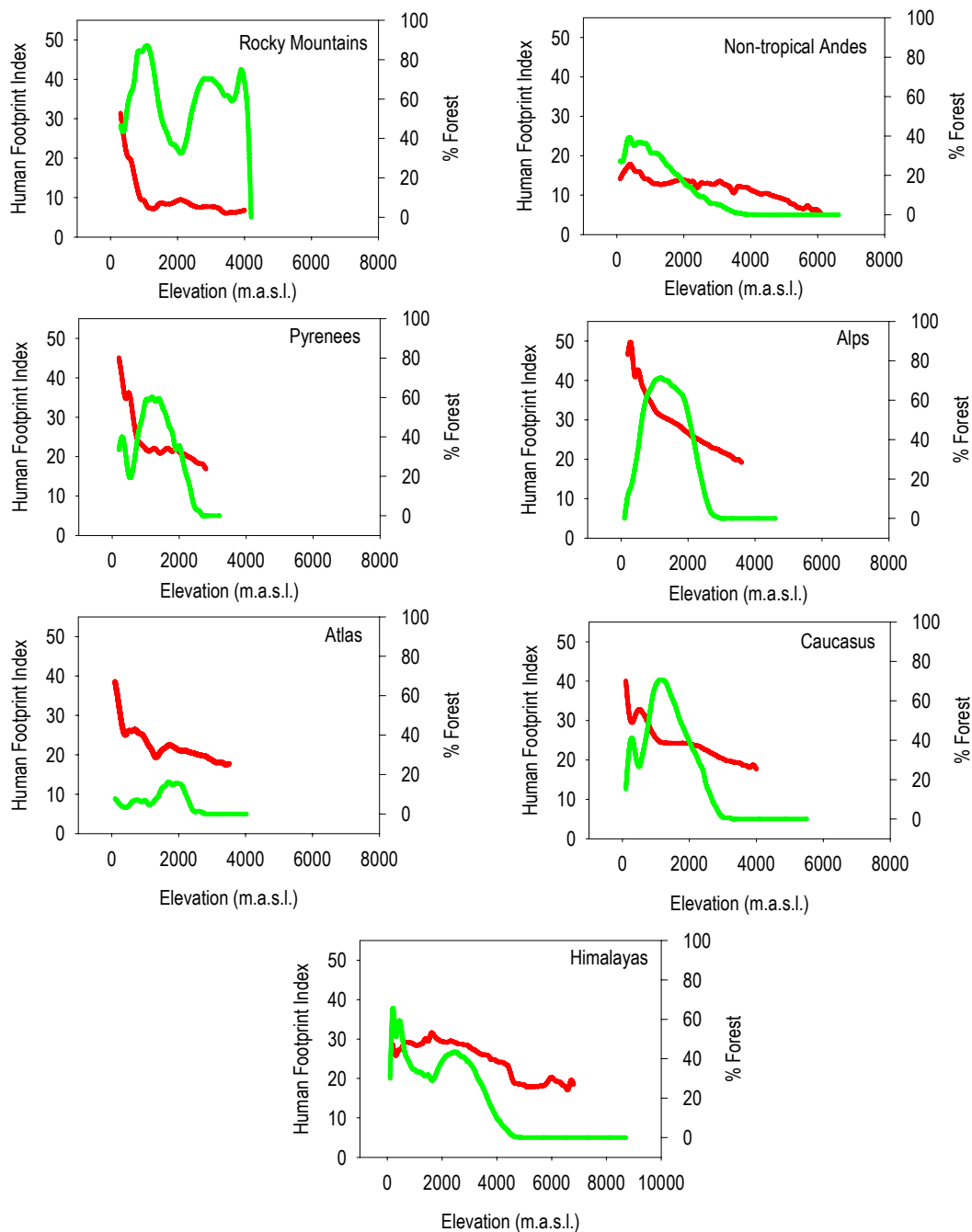


Supplementary Figure 2. Scale effects on altitudinal species richness patterns. Generated by repeated sampling of the same data set, the bivariate plots shows the empirical species richness patterns based on 25 combinations of scale of extent ( $y$ -axis) and grain size ( $x$ -axis) The surveyed gradient was limited by omitting segments from the upper limit of the gradient. The portion of the gradient sampled is illustrated by the grey shaded area in the small triangles next to the  $y$ -axis.

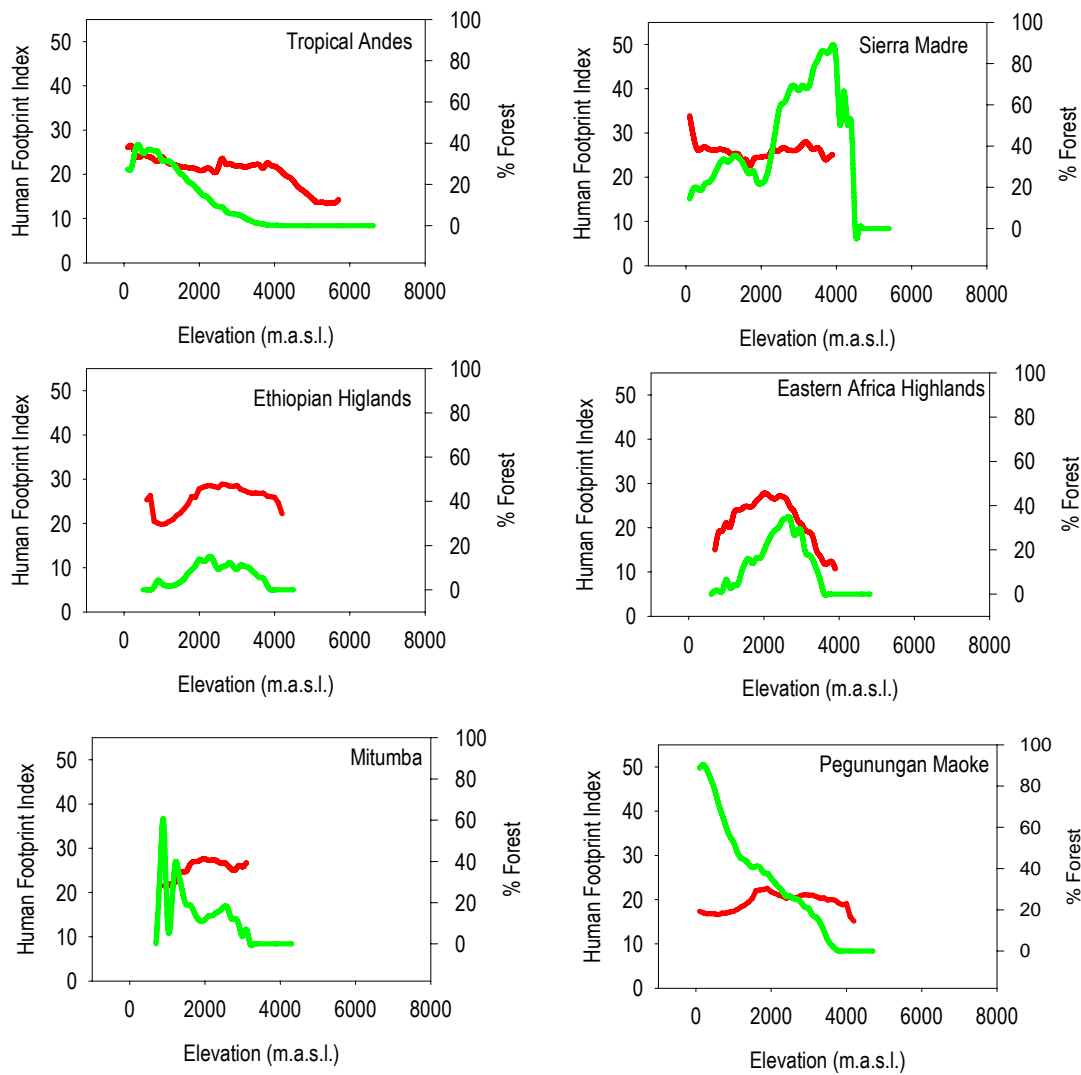


Supplementary Figure 3. Correlative fit between empirical altitudinal species richness patterns and predicted patterns from four diversity models based on data from a single-transect gradient in Costa Rica. (A). As a supplement to our two-dimensional regional Pyrenean data set, we analysis the sensitivity of patterns to scale effects in other elevational gradient (see Methods). Schematic illustration of expected species richness patterns for the four diversity models as related to productivity (Models 1 and 3), area (Model 2), and geometric constraints (Model 4); (see main text, Methods and Figure 1S for additional details on models); (B) degree of correlation (Pearson) between expected and empirical species richness values in 100-m altitudinal zones when sampling the same data with scale of

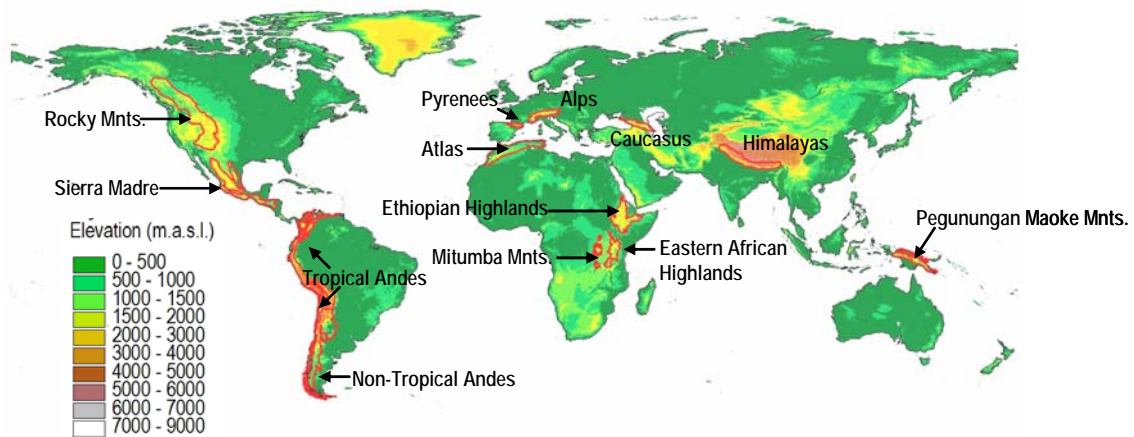
extent (omitting 0 m, 500 m, 1000 m, 1500 m, 2000 m segments from the lower limit of the gradient, as illustrated by the grey-shaded area of the small triangles next to each of the  $y$ -axes). (C) as panel B, but omitting segments from the upper limit of the gradient. (D) Colored squares indicate the model with the highest Pearson correlation (i.e. best fit) when omitting segments from the lower and upper limits of the gradient, respectively, from the analysis. Grey squares indicate combinations of extent and grain not analyzed in this study (see Methods)



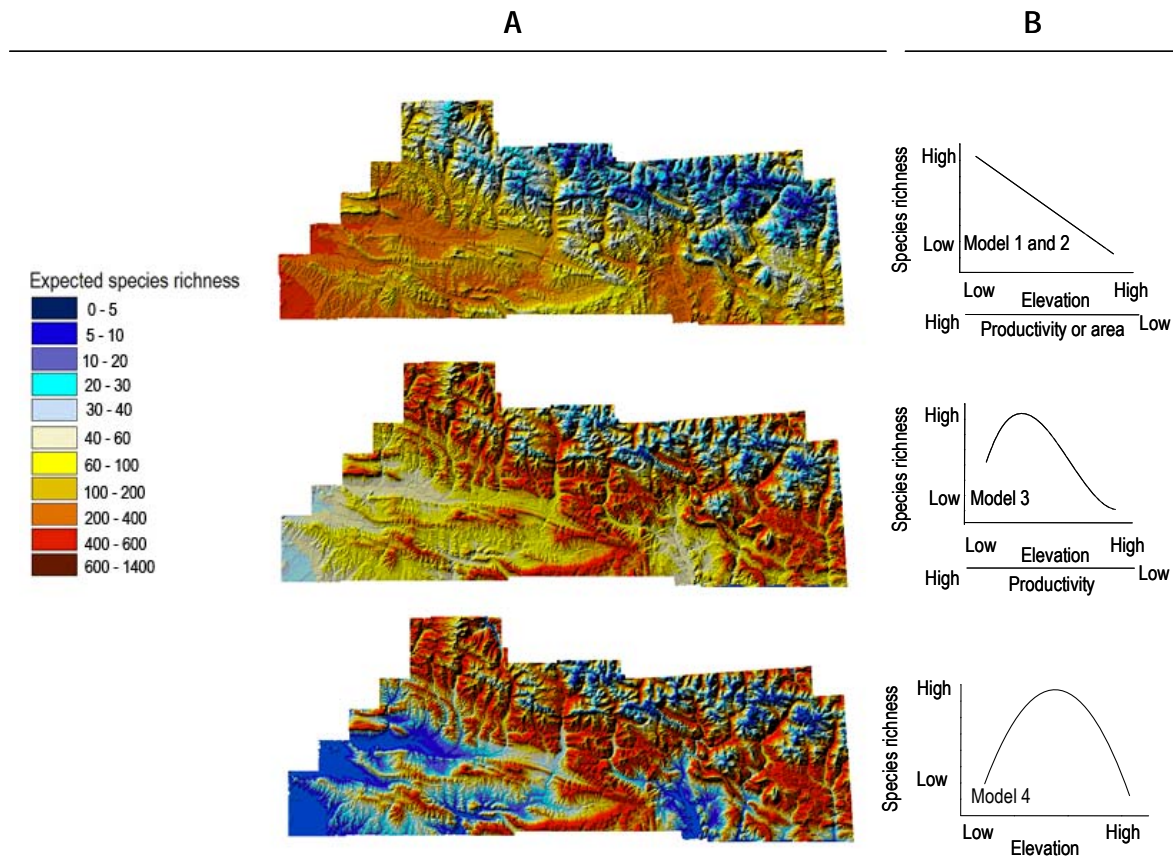
Supplementary Figure 4. Human impact along the elevational gradient in six non-tropical mountain regions. The green line indicates the percentage of area covered by forest for each elevational band of 100 meters. The red line indicates the human footprint index for each elevational band varying from 0 (least impact) to 100 (most impact). Values of human footprint index approaching 100 are usually assigned to dense urban areas. See Methods for details on data sources and analyses.



**Supplementary Figure 5. Human impact along the elevational gradient in six tropical mountain regions.** The green line indicates the percentage of area covered by forest for each elevational band of 100 meter. The red line indicates the human footprint index for each elevational band, varying from 0 (least impact) to 100 (most impact). Values of human footprint index approaching 100 are usually assigned to dense urban areas. See Methods for details on data sources and analyses.



Supplementary Figure 6. Location and identities of the 13 mountain regions analyzed and presented, either individually as in Supplementary Figures 4 and 5, or combined in Figure 3. Red lines encompass the thirteen mountain ranges analyzed. These mountain ranges represent non-tropical and tropical mountain ranges of medium to large area, from medium-altitude peaks to the world highest mountains and from different socio-economical regions of the world. The Andes were divided into tropical and non-tropical ranges at the Tropic of Capricorn ( $23^{\circ} 26' 22''$  south of the Equator).



Supplementary Figure 7. Predicted species richness patterns for a grain size of 1 km<sup>2</sup> for the four diversity models used in this study.



## Supplementary Tables

	Regional	Single transect	Total
No. of Altitudinal gradient data sets	258	203	461
No. of data sets with data points from $\leq 500$ m to $\geq 2000$ m a.s.l.	41	37	78
No. of data sets where the entire gradient has been surveyed from the valley floor to the mountain top (“complete gradient”)	41	24	65
No. of “complete gradient” data sets, with seemingly undisturbed habitats along the entire gradient	*	12	12

\* The natural habitats of all Mountain regions in the world are disturbed by anthropogenic impact in at least part of their range (see also Supplementary Figure 4 and 5)

Supplementary Table 1. Number of data sets found in the literature published since 1990, with data on the variation of species richness with altitude summarized by scale and listed for categories of completeness of gradient surveyed and anthropogenically undisturbed gradients (see Methods).

Reference	Year	Taxon	Region	Scale/ Extent	Altitudinal range <sup>1</sup>	No. Sites/ zones/ cells <sup>2</sup>	Habitat <sup>3</sup>	Shape of altitudinal richness pattern <sup>4</sup>	Details <sup>5</sup>	Sampling standardised <sup>6</sup>	Comment on lowest/highest elevations	Complete gradient <sup>7</sup>	Complete gradient with undisturbed natural habitats <sup>8</sup>
Hegazy et al	1998	Plants	Asia	Local	0-2800	5	Nonforest	Hump-shaped	Symm, peak in 500-2000 m zone	Standardised	Arid habitat	X	X
Brühl	1999	Ants	Asia	Local	500-2600	9	Forest	Decreasing		Standardised	elevations below 500 m are too disturbed		
Escobar et al.	2007	Beetles	Central America	Local	50-3000	8	Forest	Hump-shaped		Unstandardised, uses MM estimation	Apparently natural forest	X	X
Shepherd and Kelt	1999	Mammals	North America	Local	0-2600	7	Varies	Hump-shaped	Symm, peak at 1200	Unstandardised	Disturbance unknown	X	X
Kessler	2001	Acanthaceae plants	South America	Local	200-3900	20	Forest	Hump-shaped	Hump at 1000	Standardised	Disturbed below 1000m	X	
Kessler	2001	Araceae plants	South America	Local	200-3900	20	Forest	Hump-shaped	Hump at 1000	Standardised	Disturbed below 1000m	X	
Kessler	2001	Bromeliaceae plants	South America	Local	200-3900	20	Forest	Hump-shaped	Symm, peak at 2000	Standardised	Disturbed below 1000m	X	
Kessler	2001	Melastomatace ae plants	South America	Local	200-3900	20	Forest	Flat, then decreasing	Decreasing above 1500	Standardised	Disturbed below 1000m	X	
Kessler	2001	Palms	South America	Local	200-3900	20	Forest	Decreasing		Standardised	Disturbed below 1000m	X	
Kessler	2001	Ferns	South America	Local	200-3900	20	Forest	Hump-shaped	Hump at 1900m	Standardised	Disturbed below 1000m	X	
Davis et al	1999	Beetles	Africa	Local	500-2800	6	Nonforest	Flat, then decreasing	Decreasing above 1500, DWLS	Standardised	"Gradient is ""mainly natural"", no lower elevation"	X	X
Blanche and Ludwig	2001	Plants	North America	Local	500-2100	5	Varies	Hump-shaped	Symm, peak at 1400	Standardised	Gradient is ARID, no lower elevation	X	X
Blanche and Ludwig	2001	Insects	North America	Local	500-2100	5	Varies	Hump-shaped	Symm, peak at 1400	Standardised	Gradient is ARID, no lower elevation	X	X
Herzog et al.	2005	Birds	South America	Local	200-4800	12	Forest	Flat, then decreasing		Standardised	Lowest elevations deeply disturbed	X	
Kelt	1999	Mammals	North America	Local	0-2000	8	Varies	Other	2 peaks	Unstandardised	Lowest elevations disturbed	X	
Kessler	2000c	Palms	South America	Local	300-3900	36	Forest	Hump-shaped	Hump at 600	Unstandardised	Lowest elevations disturbed	X	
Krömer and Kessler	2006	Bromeliad plants	South America	Local	300-4000	8	Forest	Hump-shaped		Standardised	Lowest elevations disturbed	X	
Grytnes	2003	Plants	Europe	Local	400-2100	40	Varies	Hump-shaped	Symmetrical, peak 1100	Standardised	Lowest site 360m, elevations below are habitation		
Kessler	2000b	Palms	South America	Local	300-4000	37	Forest	Hump-shaped	Hump at 1600	Standardised	Lowest site presumably disturbed.		
Kessler	2000a	Acanthaceae	South	Local	500-2400	15	Forest	Decreasing		Standardised	Lowest sites are		

		plants	America								heavily disturbed		
Kessler	2000a	Araceae plants	South America	Local	500-2400	15	Forest	Hump-shaped	Hump at 1000	Standardised	Lowest sites are heavily disturbed		
Kessler	2000a	Bromeliaceae plants	South America	Local	500-2400	15	Forest	Hump-shaped	Hump at 1100	Standardised	Lowest sites are heavily disturbed		
Kessler	2000a	Cactaceae plants	South America	Local	500-2400	15	Forest	Hump-shaped	Hump at 1100	Standardised	Lowest sites are heavily disturbed		
Kessler	2000a	Melastomataceae plants	South America	Local	500-2400	15	Forest	Hump-shaped	Symm., peak at 1800	Standardised	Lowest sites are heavily disturbed		
Kessler	2000a	Ferns	South America	Local	500-2400	15	Forest	Hump-shaped	Symm., almost increasing, peak at 2000	Standardised	Lowest sites are heavily disturbed		
Kessler	2000b	Ferns	South America	Local	500-2500	8	Forest	Hump-shaped	Symmetrical, peak at 1800, almost increasing	Standardised	Lowest sites are heavily disturbed		
Sanders et al.	2003	Ants	North America	Local	100-2200	13	Varies	Hump-shaped	Symmetrical, peak at 1600	Standardised	Mixed habitat	X	X
Blake and Loiselle	2000	Birds	Central America	Local	0-2000	5	Forest	Decreasing		Unstandardised	Natural forest	X	X
Cardelus et al.	2006	Epiphytes	Central America	Local	30-2600	6	Forest	Hump-shaped		Standardised	Natural forest	X	X
Tattersfield et al.	2006	Snails	Africa	Local	400-2000	16	Forest	Hump-shaped		Standardised	No info in paper (Mwanihana)	X	?
Patterson et al.	1996	Bats	South America	Local	300-3400	31	Forest	Decreasing		Unstandardised	Puna at top	X	?
Escobar et al.	2007	Beetles2	Central America	Local	50-3300	7	Forest	Hump-shaped		Unstandardised, uses MM estimation	Unclear, probably disturbed at some elevations	X	
Escobar et al.	2007	Beetles3	South America	Local	450-2500	7	Forest	Decreasing		Unstandardised, uses MM estimation	Unclear, probably disturbed at some elevations, definitely disturbed below lowest site		
Brehm et al.	2007	Moths	Central America	Local	40-2730	12	Forest	Hump-shaped		Unstandardised, rarefaction	Undisturbed forest gradient	X	X
Kluge et al.	2006	Pteridophytes	Central America	Local	100-2600	>100	Forest	Hump-shaped	Symmetrical	Standardised	Undisturbed forest gradient	X	X
Lieberman et al.	1996	Trees	Central America	Local	100-2600	11	Forest	Hump-shaped	Hump at 300m	Standardised	Undisturbed forest gradient	X	X
Lomolino	2001	Plants	Asia	Local	100-2800	27	Nonforest	Hump-shaped	Hump at 1200	Unstandardised	Unknown		
Grytnes and Beaman	2006	Plants	Asia	Regional, bands, approx. Local	100-4000	14	Forest	Hump-shaped		Unstandardised	Natural forest	X	
Bachman et al.	2004	Palms	Asia	Regional, entire bands	0-5000	15	Varies	Hump-shaped	Symmetrical, but see comments		(Regional, complete coverage)	X	

Rahbek	1997	Birds	South America	Regional, entire bands	0-5000	7	Varies	Hump-shaped	Hump at 1200	(Regional, complete coverage)	X
Bhattarai and Vetaas	2006	Trees	Asia	Regional, entire bands	100-4300	40	Varies	Hump-shaped		(Regional, complete)	X
Bhattarai et al.	2004	Ferns	Asia	Regional, entire bands	100-4800	48	Varies	Hump-shaped	Symmetrical, peak at 2000	(Regional, complete)	X
Hausdorf	2006	Snails1	Europe	Regional, entire bands	0-3200	32	Varies	Hump-shaped		(Regional, complete)	X
Hausdorf	2006	Snails2	Europe	Regional, entire bands	0-2900	29	Varies	Hump-shaped		(Regional, complete)	X
Kessler	2002	Plants	South America	Regional, entire bands	0-4500	10	Varies	Decreasing		(Regional, complete)	X
Lan and Dunbar	2000	Birds	Asia	Regional, entire bands	0-5000	10	Varies	Hump-shaped	Hump at 1500	(Regional, complete)	X
Lan and Dunbar	2000	Mammals	Asia	Regional, entire bands	0-5000	10	Varies	Hump-shaped	Symm, peak at 2500	(Regional, complete)	X
Lees et al	1999	Butterflies	Africa	Regional, entire bands	0-2000	40	Forest	Hump-shaped	Hump at 1200, i.e. above midpoint	(Regional, complete)	X
Nathan and Werner	1999	Reptiles	Asia	Regional, entire bands	300-2800	25	Nonforest	Hump-shaped	Hump at 1300	(Regional, complete)	X
Nathan and Werner	1999	Birds	Asia	Regional, entire bands	300-2800	25	Nonforest	Hump-shaped	Hump at 1100	(Regional, complete)	X
Navas	2003	Herps	South America	Regional, entire bands	0-5000	50?	Varies	Hump-shaped	Hump at 1200	(Regional, complete)	X
Poulsen and Lambert	2000	Birds	Asia	Regional, entire bands	0-1800	18	Forest	Hump-shaped	Hump at 800	(Regional, complete)	X
Poulsen and Lambert	2000	Birds	Asia	Regional, entire bands	0-1800	18	Forest	Hump-shaped	Hump at 700	(Regional, complete)	X
Poulsen and Lambert	2000	Birds	Asia	Regional, entire bands	0-1500	15	Forest	Decreasing		(Regional, complete)	x
Sanders	2002	Ants	North America	Regional, entire bands	100-4400	43	Varies	Hump-shaped	Symm, peak at 2000	(Regional, complete)	X

Sanders	2002	Ants	North America	Regional, entire bands	100-4401	43	Varies	Hump-shaped	Symm, peak at 2000	(Regional, complete)	X	
Sanders	2002	Ants	North America	Regional, entire bands	100-4402	43	Varies	Hump-shaped	Hump at 1500	(Regional, complete)	X	
Smith et al.	2007	Frogs	Central America	Regional, entire bands	200-4000	8	Varies	Hump-shaped		(Regional, complete)	X	
Thiollay	1996	Raptors	South America	Regional, entire bands	100-3500	5	Varies	Decreasing		(Regional, complete)	X	
Veech	2000	Liolaemus lizards	South America	Regional, entire bands	100-5100	50	Varies	Hump-shaped	Hump at 1200	(Regional, complete)	X	
Vetaas and Grytnes	2002	Plants	Asia	Regional, entire bands	200-6000	50	Varies	Hump-shaped	Hump at 2000	(Regional, complete)	X	
Wiens et al.	2007	Salamanders	Central America	Regional, entire bands	200-5000	10	Varies	Hump-shaped		(Regional, complete)	X	
Wolf and Flamenco-S	2003	Epiphyte plants	Central America	Regional, entire bands	0-4000	6	Varies	Hump-shaped	Humpshaped, peak at 1000-1500	(Regional, complete)	X	
Fu et al.	2004	Fish	Asia	Regional, entire bands	0-5000	50	River	Declining	Small hump?	River....	X	
Leimbeck et al.	2004	Araceae plants	South America	Regional, grids	0-5000	2076	Varies	Decreasing	?	(Regional, complete coverage)	X	
Lobo et al	2001	Plants	Europe	Regional, grids	0-3500	254	Varies	Increasing		(Regional, complete coverage)	X	
Pausas and Saez	2000	Ferns	Europe	Regional, grids	0-3000	5	Varies	Increasing		(Regional, complete coverage)	X	
Keeley et al	2003	Plants	North America	Regional, scattered points	400-2500	128	Varies	Decreasing		Standardised	Lowest site is 440 m, no lower elevation inside park.	X
Zhao et al.	2005	Plants	Asia	Regional, scattered points	470-3100	161	Forest	Hump-shaped		Standardised	Apparently natural forest and no lower elevation in region, which is a single mountain range	X
Lacoul and Freedman	2006	Aq. Plants	Nepal	Regional, scattered points	100-4700	28	Lakes	Hump-shaped		Unstandardised	Discusses intermediate disturbance hypothesis, but unclear about disturbance of low elevation lakes.	X

Tallents et al.	2005	Trees	Africa	Regional, scattered points	280-2180	231	Forest	Hump-shaped		Standardised	Low elevations disturbed	X
Lovett	1996	Trees	Africa	Regional, scattered points	300-2200	363	Forest	Decreasing		Unstandardised	Lowest elevations disturbed	X
Patterson et al	1998	Birds	South America	Regional, scattered points	400-3400	13	Forest	Decreasing		Unstandardised	Puna at top	X
Patterson et al	1998	Bats	South America	Regional, scattered points	400-3400	13	Forest	Decreasing		Unstandardised	Puna at top	X
Patterson et al	1998	Murids	South America	Regional, scattered points	400-3400	7	Forest	Other	Peaks at 400 and 3400	Unstandardised	Puna at top	X
Jacquemyn et al.	2005	Orchids	Africa (Reunion)	Regional, scattered points	100-2500	121	Varies	Hump-shaped	Authors claim monotonic decrease...	Standardised	Regional study, but in general lowlands are disturbed ,and few datapoints from lowlands	X
Lee et al.	2004	Birds	Asia	Regional, scattered points	0-3500	674	Varies	Hump-shaped	Humpshaped, peak at 2000m	Standardised	Regional, authors say many low sites maybe disturbed	X
Menni et al.	2005	Fish	South America	Regional, scattered points	400-3800	26	River	Hump-shaped		Unstandardised	River systems, no lower elevation in region	X

<sup>1</sup> Describes the extent from lowest to highest sampling point.

<sup>2</sup> Lists the total number of sampling points, grids or bands used to presenting the altitudinal species richness pattern in the study.

<sup>3</sup> Lists the main habitat type of the gradient.

<sup>4</sup> Describes the overall pattern as depicted in the paper<sup>cf procedure of 44</sup>. A hump-shaped shape can either be a pattern with a symmetrical peak or a skewed hump.

<sup>5</sup> Outlines additional information on the altitudinal species richness pattern

<sup>6</sup> Lists if data were attempted collected by a standardised or non-standardised sampling protocol <sup>cf procedure of 44</sup>. It is noted if data were subsequently adjusted by species richness estimation methods.

<sup>7</sup> An "X" indicates that the entire gradient has been surveyed from the valley floor to the mountain top ("complete gradient")

<sup>8</sup> An "X" indicates that, judged from the description in the individual papers, the gradient data sets may have natural undisturbed habitat along the entire gradient.

**Supplementary Table 2.** This table contains an overview of the 78 gradient data sets with data points from  $\leq 500$  m to  $\geq 2000$ . The single-gradient studies are listed first followed by data on the regional studies.

## Supplementary notes

### Supplementary References

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