

LETTERS

Scale effects and human impact on the elevational species richness gradients

D. Nogués-Bravo^{1,2,3}, M. B. Araújo^{1,2}, T. Romdal² & C. Rahbek²

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^{1–3}. 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^{1,4,5}. However, since the more recent general acceptance of altitudinal gradients as model templates for testing hypotheses behind large-scale patterns of diversity^{5–9}, 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 connected¹⁰. 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 studies⁹. 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 controversial³. 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 distributions⁹. It has therefore been suggested that non-generality in altitudinal species richness patterns may be a result of differences in spatial design between studies⁹. 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^{11,12}, area^{8,13,14} and, more recently, geometric constraints^{8,15} have been used as support for competing hypotheses^{5,9,13,16,17}.

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^{5,9}. 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 richness¹⁸.

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 gradients¹⁵. 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).

¹Department of Biodiversity and Evolutionary Biology, National Museum of Natural Sciences, CSIC, C/ José Gutiérrez Abascal, 2, 28006 Madrid, Spain. ²Center for Macroecology, Institute of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. ³Pyrenean Institute of Ecology, CSIC, Avda. Montañana, 1005, 50080 Zaragoza (Zaragoza), Spain.

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 gradient¹⁹. It has long been recognized that truncation of a gradient may affect species richness patterns²⁰, whereas tabulation of the shape of the pattern of altitudinal species richness has suggested that these may be sensitive to scale effects⁹. 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 gradient²¹. 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 universal²², as we obtain the same results when repeating our analyses with a data set from Costa Rica²³, 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 intercorrelated⁹, and the absence of suitable factorial techniques²⁴ 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 analysis¹⁸ 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)^{1,4,5}. Today, with more than 1,000 studies⁹, 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^{5–9,11,13,16,17}. 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.

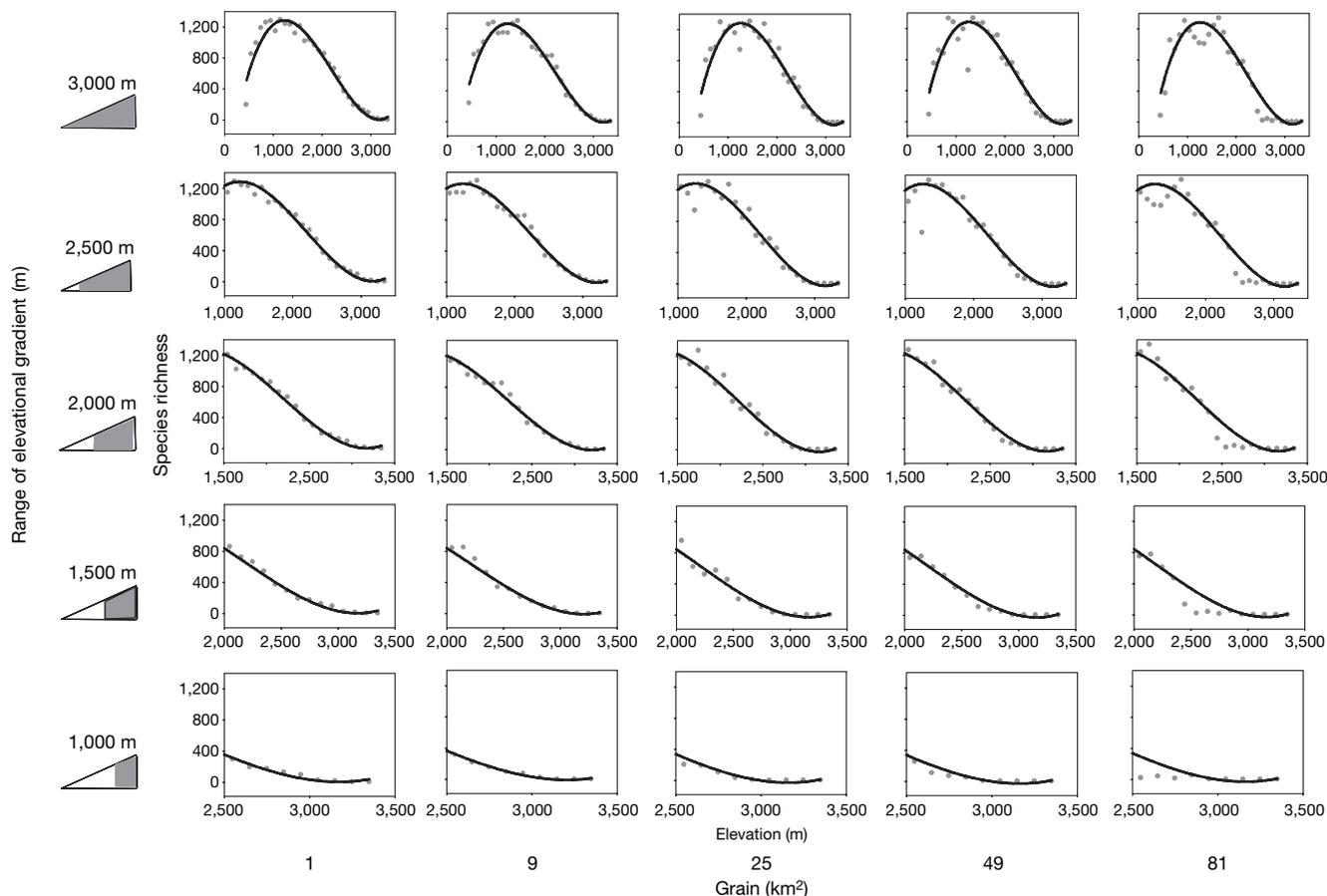


Figure 1 | Scale effects on altitudinal species richness patterns. These bivariate plots, generated by repeated sampling of the same data set, show the empirical species richness patterns based on 25 combinations of scale of extent (y axis) and grain size (x axis). The surveyed gradient was reduced by

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 lowlands⁵. 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 specialists²⁵.

To manage biodiversity, today and in the future, it is crucial to understand the processes behind the observed natural patterns of biodiversity²⁶. 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.

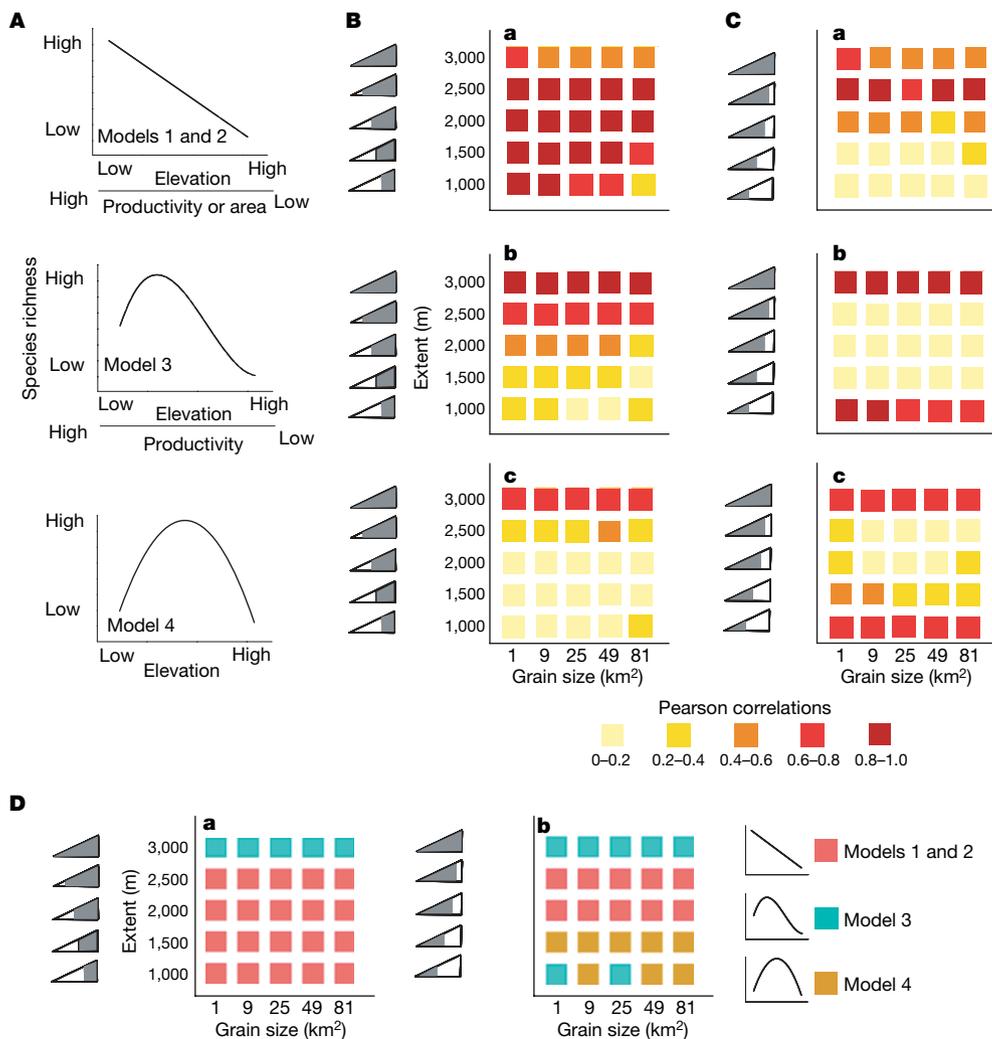


Figure 2 | Scale effects on patterns of altitudinal species richness and testing of four generalized diversity models. **A**, Schematic illustration of expected species richness patterns for four diversity models (see the text, Methods and Supplementary Fig. 1 for additional details on models). **B**, 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 km²) 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. **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.

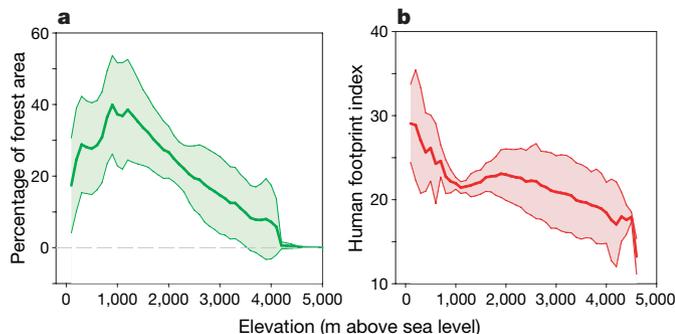


Figure 3 | Worldwide and generalized pattern of human impact along the altitudinal gradient. **a**, The bold green line indicates the percentage of area covered by forest (natural vegetation). **b**, The bold red line indicates the averaged human footprint index for each elevational band of 100 m above 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 ± 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 bryophytes²⁷ from the central Spanish Pyrenees (13,500 km²) 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 software²⁸, 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-km² 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.

Received 26 December 2007; accepted 4 February 2008.

- Rohde, K. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**, 514–527 (1992).
- Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, 1995).
- Willig, M. R., Kaufman, D. M. & Stevens, R. D. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273–309 (2003).
- MacArthur, R. *Geographical Ecology* (Princeton Univ. Press, Princeton, NJ, 1972).
- Rahbek, C. The elevational gradient of species richness—a uniform pattern. *Ecography* **18**, 200–205 (1995).

- Heaney, L. R. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecol. Biogeogr.* **10**, 15–39 (2001).
- Lomolino, M. Elevation gradients of species-density: historical and prospective views. *Global Ecol. Biogeogr.* **10**, 3–13 (2001).
- Sanders, N. J. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography* **25**, 25–32 (2002).
- Rahbek, C. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* **8**, 224–239 (2005).
- McNeill, J. R. *The Mountains of the Mediterranean World* (Cambridge Univ. Press, Cambridge, 1992).
- Sanders, N. J., Moss, J. & Wagner, D. Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecol. Biogeogr.* **12**, 93–102 (2003).
- Bhattarai, K. R., Vetaas, O. R. & Grytnes, J. A. Fern species richness along a central Himalayan elevational gradient, Nepal. *J. Biogeogr.* **31**, 389–400 (2004).
- Rahbek, C. The relationship among area, elevation, and regional species richness in neotropical birds. *Am. Nat.* **149**, 875–902 (1997).
- Romdal, T. S. & Grytnes, J. A. An indirect area effect on elevational species richness patterns. *Ecography* **30**, 440–448 (2007).
- Colwell, R. K., Rahbek, C. & Gotelli, N. J. The mid-domain effect and species richness patterns: what have we learned so far? *Am. Nat.* **167**, E1–E23 (2004).
- Dunn, R. R., McCain, C. M. & Sanders, N. J. When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. *Global Ecol. Biogeogr.* **16**, 305–312 (2007).
- McCain, C. M. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecol. Biogeogr.* **16**, 1–13 (2007).
- Rahbek, C. & Graves, G. R. Multiscale assessment of patterns of avian species richness. *Proc. Natl Acad. Sci. USA* **98**, 4534–4539 (2001).
- Chase, J. M. & Leibold, M. A. Spatial scale dictates the productivity–biodiversity relationship. *Nature* **416**, 427–430 (2002).
- McCoy, E. D. The veiled gradients problem in ecology. *Oikos* **99**, 189–192 (2002).
- McCain, C. M. Area and mammalian elevational diversity. *Ecology* **88**, 76–86 (2007).
- Whittaker, R. J., Willis, K. J. & Field, R. Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.* **28**, 453–470 (2001).
- Brehm, G., Colwell, R. K. & Kluge, J. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecol. Biogeogr.* **16**, 205–219 (2007).
- Hillebrand, H. On the generality of the latitudinal diversity gradient. *Am. Nat.* **163**, 192–211 (2004).
- Connell, J. H. Diversity in tropical rain forests and coral reefs—high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* **199**, 1302–1310 (1978).
- Mace, G. M. *et al.* It's time to work together and stop duplicating conservation efforts.... *Nature* **405**, 393 (2000).
- Pyrenean Institute of Ecology. *Atlas de Flora de Aragón* (<http://www.ipe.csic.es/floragon/index3.php>) (2005).
- Clark Labs. *Idrisi Kilimanjaro version 14.02. GIS software package* (Clark Labs, Clark University, Worcester, MA, 2004).

Supplementary Information is linked to the online version of the paper at 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.

Author Information Reprints and permissions information is available at www.nature.com/reprints. Correspondence and requests for materials should be addressed to D.N.B. (davidnagues@mncn.csic.es).

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 software²⁸.

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'²⁹, 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 Kilimanjaro²⁸ (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.

29. Sanderson, E. W. *et al.* The human footprint and the last of the wild. *Bioscience* 52, 891–904 (2002).