

An indirect area effect on elevational species richness patterns

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The study of elevational diversity patterns, and the attempt to disentangle the factors that create them, has proved a challenging and controversial research venue over the last few decades (Terborgh 1977, 1985, Stevens 1992, Rahbek 1995, 1997, 2005, Körner 2000, Brown 2001, Lomolino 2001, McCain 2005). Studies of elevational gradients fall into two general categories, regional studies that summarize known distributions from complete elevational bands (zones) within a defined geographical or political region, and local-scale transect studies that are based on a single survey scheme (Rahbek 1995, 2005). Elevational band area (the compiled area of each elevational zone) of a mountainous region is generally expected to decline with altitude (MacArthur 1972, Körner 2000, Lomolino 2001), although the smallest area per elevational zone can also be found at mid-elevation, where slope is sometimes steeper (Rahbek 1997). That area of regional elevational bands can influence the number of species found in each band was first clearly demonstrated by Rahbek (1997), and several studies since then have explicitly investigated this regional area effect on elevational diversity gradients (Sanders 2002, Sanders et al. 2003, Bachman et al. 2004).

In recent years there has been a renewed interest in the analysis of standardized species richness data sets from transects in order to evaluate simultaneously the potential drivers of elevational diversity gradients (Md. Nor 2001, Sanchez-Cordero 2001, Grytnes 2003, Kattan and Franco 2004, Herzog et al. 2005). A number of factors such as climate-derived productivity, source-sink dynamics and the mid-domain effect, have been evaluated, and the diversity of results confirm the belief that no single factor is responsible for all observed richness patterns (Rahbek 1995, 2005, Brown 2001, Lomolino 2001, McCain 2006, Dunn et al. 2007).

Most transect studies attempt to control the influence of area by sampling equal-area plots, although unstandardized plots also frequently occur (Lieberman et al. 1996, Hoffmann et al. 2001, Herzog et al. 2005). However, in addition to the direct influence of the area of the sampled plot, local communities can be perceived as dynamic samples drawn from a regional species pool (Terborgh 1973, Graves and Gotelli 1983, Cornell 1985, Ricklefs 1987). The size of the surrounding region can be thought of as a surrogate variable for the size of the regional species pool (Terborgh and Faaborg 1980, Cornell and Lawton 1992, Caley and Schluter 1997, Cornell 1999). This additional effect of area on elevational transects was, to our knowledge, first discussed by Beehler (1981), who found that a linear decrease in New Guinean forest birds on an elevational transect was paralleled by a decrease in regional area. Several other authors have suggested that regional habitat area influenced observed elevational richness patterns (Holloway 1987, Stotz 1998, Patterson et al. 1998, Brehm et al. 2003), while Heaney (2001) and Sanders et al. (2003) presented results contrasting with the hypothesis. Some recent studies have attempted to analyse this area effect quantitatively. Grytnes (2003) found that elevational band area was only correlated with site richness in two out of seven elevational gradients of plant richness in Norway. In contrast, a considerable influence from measures of surrounding habitat area has recently been demonstrated on a tropical transect measuring avian richness (Herzog et al. 2005).

We will use the term indirect area effect to describe the effect of regional area on the pattern of local species richness. In an attempt to quantitatively evaluate the importance of the indirect area effect we have performed a meta-analysis on data from 71 elevational

richness patterns using all available studies of single transect gradients found in the literature.

The hypothesis of an indirect area effect

We use the term local to designate the scale at which sampling is done at one site along an elevational transect, and regional to apply to the entire elevational band or zone (Fig. 1). We will explore the complex relationships linking regional area (A_R), regional species richness (S_R), local area (A_L), and local species richness (S_L) for elevational gradients by building on two premises. First, the number of species in an elevational band (S_R) is influenced by band area (A_R) through the Arrhenius equation (Arrhenius 1921, Connor and McCoy 1979). Second, the number of species in a plot (S_L) is correlated with the regional richness (S_R). The latter relation can be linear or nonlinear (Graves and Rahbek 2005, He et al. 2005), and has been described mathematically in several versions (Rosenzweig and Ziv 1999, He et al. 2005). Combined, these two well known effects predict a linear relation between log-area of regional bands (A_R) and log-richness of plots (S_L) (Rosenzweig and Ziv 1999).

We therefore use the following working hypothesis to test for what we will term the indirect area effect for local-scale elevational richness patterns: the number of species in equal-area plots S_L on elevational transects is correlated with the area of the surrounding elevational zone A_R , such that

$$\log S_L = z \log A_R + c \quad (1)$$

where z is the slope on log-log scale, and c is a constant. This equation is identical to the Arrhenius equation for a “direct” area effect because we merely combine the Arrhenius equation with a linear relation.

Meta-analysis on forest transect data

Our aim is to quantify the strength of the relationship between local species richness and regional habitat area, and we are as such not interested in exact parameterizations of z and c in eq. 1. To measure the strength of the A_R - S_L -relation we used the Pearson correlation coefficients relating observed species richness in samples to the forest area of elevational zones. Data are from a complete survey of literature studies (Rahbek 2005), performed on the ISI Web of Science 18 April 2005 using the following search terms (including variants): (elevation OR altitude) AND (richness OR diversity). This initial search produced 1650 papers, of which only a small minority contained relevant data.

For inclusion in the database we considered only studies containing point diversity data from single forested elevational transects. The full list can be seen in the Appendix. A study was included in our analysis only if plot area and sample effort (e.g. number of trap nights or transect walks) varied at most by a factor 1.5, the transect contained a minimum of four sample sites and constituted an elevational gradient of at least 800 m. Furthermore, richness data should be readily available in the paper, and the locality described with enough precision for us to place it correctly within our forest area dataset. We restricted the analysis to forested gradients to avoid several biases. Forest extent is relatively easily defined, and forest species are often specialised to that habitat. Combining studies from different habitats is problematic, because the degree of habitat structuring greatly influences species-area relations (Drakare et al. 2006). In some cases we discarded single sites that were from other habitats, as detailed in the Appendix. We excluded studies that only analysed a subset of the taxon group in question (e.g. restricted-range species), as well as forest disturbance studies. Our

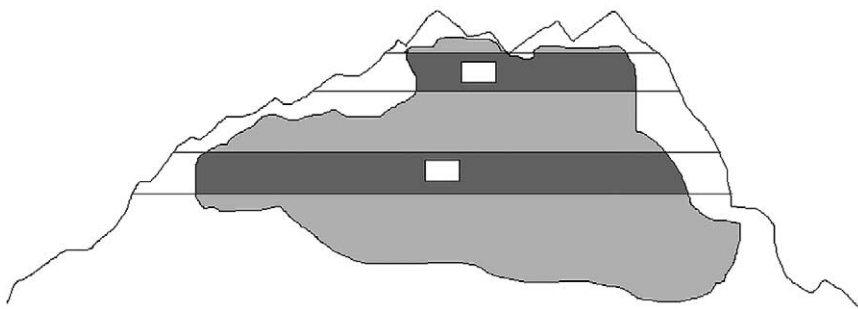


Fig. 1. The concept of the indirect area effect, as shown for a hypothetical mountain range. At each of two elevations, a standardised plot is sampled for species richness (white rectangles). Two elevational bands (horizontal lines) are outlined. The forest habitat (shaded) of each band holds the potential species pool for the sampled plot. The contiguous area of habitat differs between bands resulting in different number of species in the species pool for each plot. This in turn influences the number of species in the plots.

criteria allowed us to include 71 out of 95 local-scale forest studies.

The data on forest area were extracted from the MODIS 44b Global 500 m ISIN Grid data set, available from <http://edcdaac.usgs.gov/modis/mod44b.asp>. This global dataset was compiled from satellite data from the years 2001 and 2002. The information used was percentage of forest canopy cover in 500 × 500 m surface area cells based on a integerized sinusoidal projection. Two criteria had to be applied in order to estimate the forest areas (Appendix 1). First, forest was as our default defined as habitat having > 50% canopy cover. Second, to delimit individual forest units, we used a criterion of including all forest cells that were connected by direct contact with neighbouring forest gridcells. We made a range of sensitivity tests for other values than the defaults (Appendix 2). The overall results remained very robust to changing these criteria.

Forest area in each elevational band was derived by combining the data on forest distribution with elevational data from the Shuttle Radar Topography Mission, available at <http://glcf.umiacs.umd.edu/data/srtm>. By overlaying these two data sets we were able to identify the elevation of all forested gridcells. From this we estimated contiguous forest area of 200 m wide elevational bands centered around each empirical species richness sample point.

We performed a standardized and weighted meta-analysis of the relation between regional forest area and local species richness (Gurevitch and Hedges 1999, Gurevitch et al. 2001). The effect size variable z is a transformation of the correlation coefficient r , where

$$z = \frac{1}{2} \ln \left(\frac{1+r}{1-r} \right)$$

Values of z are expected to approximate a normal distribution. The variance of z is measured as

$$v_z = \frac{1}{N-3}$$

We then calculate a weighted average effect size \bar{Z} as

$$\bar{Z} = \frac{\sum_{i=1}^n \frac{1}{v_i} z_i}{\sum_{i=1}^n \frac{1}{v_i}}$$

with the variance of \bar{Z} being

$$s^2 = \frac{1}{\sum_{i=1}^n \frac{1}{v_i}}$$

and the confidence intervals

$$CI = \bar{Z} \pm t_{\alpha/2(n-1)}(s)$$

(Gurevitch et al. 2001). The z -values are back-transformed to r -values before presentation in tables.

A measurable effect

Of the 71 transects included, 32 were on plants, 27 were on vertebrates and 12 on invertebrates. A general pattern of species richness is not evident. For instance, there are two studies from Mt. Isarog on Luzon, one concerning ants (Samson et al. 1997) and the other mammals (Heaney 2001), which show almost opposite patterns in elevational diversity. Furthermore, the individual studies showed a wide variety of regional area vs local species richness relationships from highly positive correlations to negative correlations. In most studies there was a considerable positive correlation between forest area and local species richness, and averaging values from both positive and negative correlations yields a positive average correlation coefficient of 0.63 (Table 1). Figure 2 shows some examples of both hump-shaped and monotonically decreasing patterns of area and species richness. Patterns of decreasing species richness are mostly very well

Table 1. Correlation coefficients of the relation between surrounding habitat area and species richness, overall and for taxonomic subgroups.

Group	Number of studies	r	Lower 95% limit	Upper 95% limit
Overall	71	0.631	0.565	0.689
Invertebrates	12	0.836	0.673	0.921
Birds	13	0.903	0.826	0.947
Non-volant mammals	11	0.294	-0.092	0.603
Bats	2	0.847	-0.592	0.996
Higher plants	27	0.588	0.485	0.674
Cryptogames	5	0.233	-0.094	0.515

Herptiles (1 data set) not shown. All tests performed with the default forest definition. Averages and confidence limits were retransformed from z to r -values following analysis.

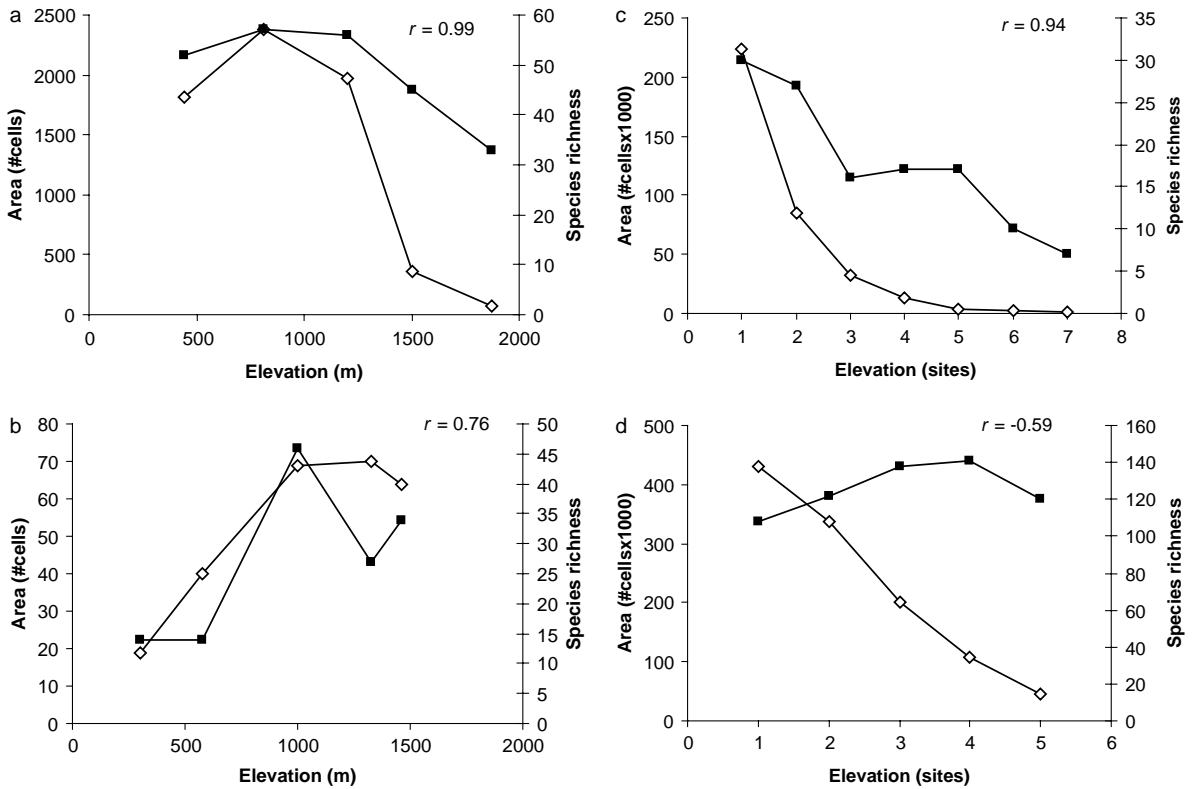


Fig. 2. Examples of the relation between elevational band area and local species richness in individual studies used for the meta-analysis. In these figures actual number of species and actual area (gridcells) is shown, while in correlation analysis logtransformed values were used. Open diamonds = forest area. Closed squares = species richness. r = Pearson correlation coefficient. (a) Bird species in Andohahela, Madagascar (Hawkins 1999). (b) Mites in Nebrodi Mts, Sicily (Migliorini and Bernini 1999). (c) Birds on Whiteface Mt., New York (Able and Noon 1976). (d) Plants in Santa Catalina Mts, Arizona (Whittaker and Niering 1975).

predicted by the area effect, whereas for hump-shaped patterns our results are more variable.

Many meta-analyses are haunted by a compilation of test values that are not obtained through identical test procedures among studies (Gurevitch et al. 2001). This is probably not a problem in our case because we obtained the values for the predictor variable, area, from an independent and standardized source, and because we limited our survey to standardized point richness data sets. One problem we do have is that some of the transects used in our analysis come from the same publications and could be said to be pseudo-replicates because they represent adjacent transects or related taxa within a single study. We made a series of sensitivity analyses to investigate these potential non-independence problems, by excluding the concerned studies. The main bias encountered was that the results for higher plants are disproportionately driven by two studies (Kessler 2000b, 2001), but our overall conclusions are not influenced.

Additional analyses

We posit a number of testable secondary hypotheses that offer further insight into the indirect area effect and its relation to other biogeographical patterns.

1) The indirect area effect should be stronger for larger spatial grain sizes than for smaller spatial grains

In a tiny plot the number of species is more constrained by the low number of individuals than by the number of species in the species pool (Connor and McCoy 1979, Rosenzweig 1995). Studies with small grain size will therefore tend to exhibit less variation in number of species among sites. This bias would apply to all hypothetical determinants, including indirect area effects. Accordingly, we found a positive linear relationship between z (strength of the indirect area effect) and

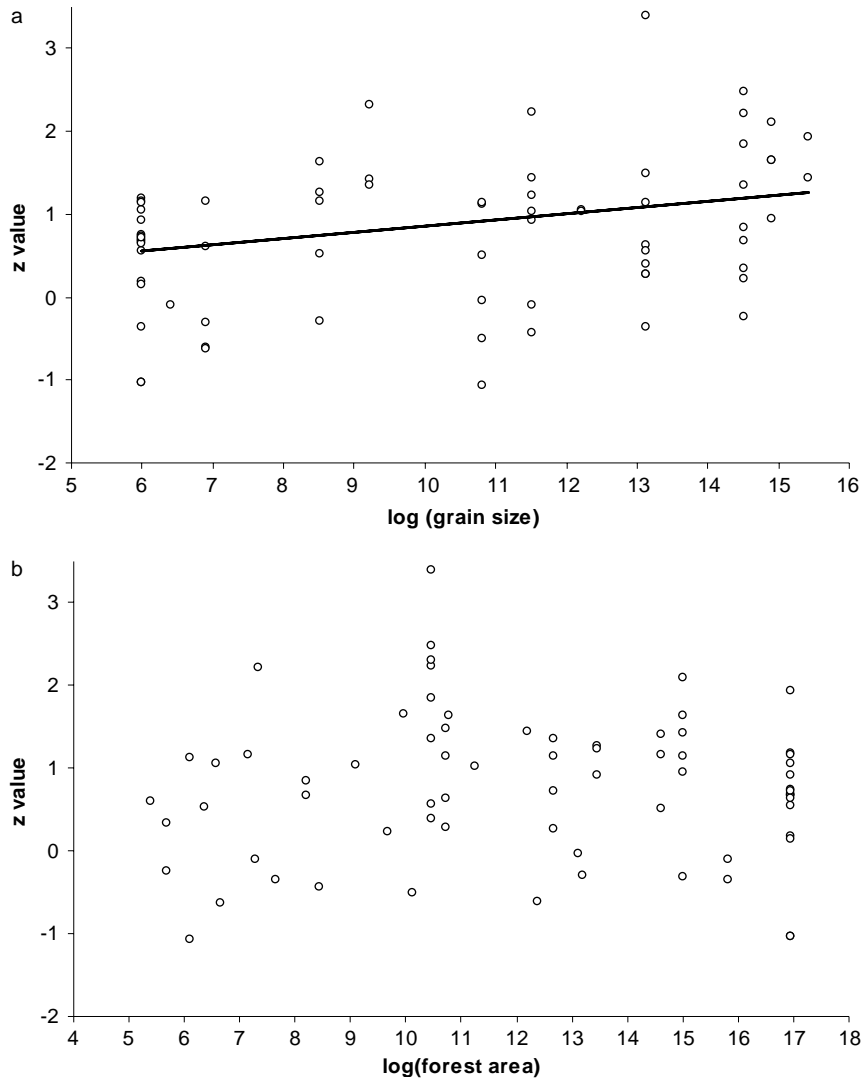


Fig. 3. The relationship between z (the transformed correlation coefficients) and log-transformed grain size (km^2) (a) and log-transformed total size area of forest (500×500 m pixels) (b). A linear relationship using weighted least square was tested. For grain size a significant linear relationship with z is found ($p = 0.0031$; $z = 1.14 + 0.076 \times \log \text{Grain size}$). No linear relationship between z and total area is found ($p = 0.77$).

Table 2. Correlation coefficients for the climate zone and dispersal subgroups.

Category ^a	Number of studies	r	Lower 95% limit	Upper 95% limit
Tropical	44	0.630	0.555	0.695
Subtropical	9	0.565	0.241	0.775
Temperate	18	0.680	0.475	0.815
High dispersal	28	0.724	0.630	0.800
Low dispersal	43	0.567	0.473	0.649

^aSubtropical category includes studies from Mexico and Taiwan. High dispersal ability group includes only volant animals and cryptogames (spores). All tests performed with default forest definition. Averages and confidence limits were retransformed from z to r -values following analysis.

the grain size used in the study, i.e. less influence for the smallest grains (Fig. 3a).

2) The indirect area effect should be stronger for smaller forests than for larger forests

We sum the area for contiguous forests under the assumption that the entire forest represents the immediate species pool for the sampled sites, even for forest areas as large as the Amazon region. Such immense forest areas will have relatively large regional area measured for all elevational bands, meaning that all bands will have large potential species pools, and the variation in area among bands should be less important.

The data did not show any support for this hypothesis when testing for a linear relationship between forest size and z (Fig. 3b). However, a visual inspection of the graph indicates that both for the smallest and largest forest sizes there is less effect, and an ad hoc second order polynomial test confirms this (unimodal pattern, $p < 0.01$). Thus for forests $> 2000 \text{ km}^2$ the pattern is qualitatively similar to what is predicted, but the smallest forests do not show a high indirect area effect. We tentatively suggest that some of the small forests from which we have data (Mt. Kenya, Mt. Elgon, Mt. Isarog on Luzon, Mt. Vermion in Greece, Haleakala on Hawaii, Mexican forests) have been reduced in elevational extent, or even isolated as forest fragments, by human activities in the twentieth century or earlier. The elevational patterns of species richness therefore do not reflect the current habitat area.

3) High latitude data sets should show a stronger effect than low latitude data sets

Species-area relations have shown to be weaker in areas with high available energy, as high number of individuals results in high species richness at all scales (Storch et al. 2005). Accordingly, we expect less influence from variation of area among bands in tropical than in temperate elevational data sets. We did not find such a trend, as studies from tropics, subtropics and temperate regions showed equal effect (Table 2).

4) The magnitude of the indirect area effect should be correlated with dispersal ability

Taxa that have potential for long distance dispersal should be less influenced by the area of isolated forests, since they will be more able to cross gaps. With a crude distinction between high-dispersal organisms (volant animals and cryptogams) and low-dispersal organisms (all other), we found a trend in accordance with this

hypothesis, but the result was statistically insignificant (Table 2).

5) The effect will differ between different taxonomic groups

Certain taxon groups are under particular habitat restrictions which should predictably be more influential than other environmental factors. Since it is against the concept of meta-analysis to exclude particular taxa (Gurevitch et al. 2001, Mittelbach et al. 2003), we instead evaluated the variation within our results by analysing taxon groups separately. Invertebrates, birds and bats (containing between them all the volant animals) are the taxon groups that have the highest r values, all above 0.8 (Table 1). Non-volant mammals and cryptogam organisms show relatively small effects of indirect area, in both cases – and for all individual studies – the peak of diversity lies at higher elevations than predicted from the area factor. For cryptogams, basic physiological restrictions normally necessitate species to occupy humid conditions, and the most humid elevations are typically above 1000–1500 m (Kessler 2000a, Kuper et al. 2004, Cardelus et al. 2006). Non-volant mammals have been speculated to share this climatic predisposition (McCain 2005), and small mammals have been speculated to be less successful at low elevations where ants are abundant competitors, based on patterns observed on tropical Asian transects (Samson et al. 1997, Heaney 2001, Md. Nor 2001).

Conclusions and implications

The indirect area effect has considerable potential as a basic influence on elevational diversity gradients. Although there is considerable variation among studies, the overall trend is a high correlation between surrounding forest area and the number of species found in sites. Elevational diversity patterns that are monotonically decreasing or nearly so (as in Fig. 2a, c) are usually well predicted by the hypothesis, as are some gradients with mid-domain peaks, especially for forest areas of small size (as in Fig. 2b). The cases where we see the least explanatory power are for some of the largest forest units we have defined, which are the entire Neotropical and Nearctic (eastern and western) forest masses. For those forest units the lowlands are by far the elevation with largest area, but elevational richness gradients in associated mountain ranges can often show pronounced midelevational peaks (as in Fig. 2d). In such cases our approach of defining the relevant regional area may not be the optimal approach.

In this study we have correlated area with diversity in a variety of taxa, while other studies have explored mathematically how local species richness levels can be predicted from the size of regional richness pools (Rosenzweig and Ziv 1999) or from the regional area (He et al. 2005). Constructing a regional species pool is problematic and requires a precise knowledge of distributions for all species, both regarding elevational and geographical limits. Because of variation in isolation and speciation events, high elevations have the largest turnover of allopatric species within a region, but such species are not all potential colonizers (Graves 1985, 1988, Brehm et al. 2003). Predicting diversity levels from species pools mathematically requires determination of z values of species-area relations (Rosenzweig and Ziv 1999, He et al. 2005). Such exact parametrisation should rest on extensive knowledge of the structural complexity and heterogeneity of the habitat type, since, even among different forest types differences occur (Drakare et al. 2006). Nevertheless, attempts to explore the exact relation of regional and local richness levels with predictive models for specific case studies could further advance this field.

Together with the fact that the highest correlation was found under the most strict forest definition criterion (Appendix) we suggest that the indirect area effect has the largest influence on elevational diversity gradients at small regional scales rather than at continental scales. The fact that patterns for some gradients, and some organisms, could not be predicted by the hypothesis, also points to the importance of other factors. Among these are the Mid-domain effect (MDE, Colwell and Hurr 1994, Colwell et al. 2004) and species-energy hypotheses (Evans et al. 2005). MDE has been promoted as a potentially strong explanation for mid-elevational species richness peaks along some gradients (Rahbek 1997, Grytnes and Vetaas 2002, Grytnes 2003, Dunn et al. 2007). However, a recent meta-analysis showed only a weak correlation between MDE and empirical patterns for elevational gradients, and it was suggested that MDE is more important on larger scales than on smaller spatial scales (Dunn et al. 2007). Energy and climate correlates are generally considered to predict monotonically decreasing patterns (Rahbek 1995), but climate can predict other elevational diversity patterns as well, depending on the interaction between energy availability and water availability (McCain 2006). The fact that many elevational patterns are neither monotonically decreasing nor mid-domain peaked, but skewed or hump-shaped (Rahbek 1995, 2005), indicates that several factors may work in concert to determine patterns in species richness. The results from our meta-analyses suggest that area within an elevational band may have a strong effect on species richness patterns along elevational gradients even when a

constant plot size and standardized sampling is used among sampling points. Future study designs should concentrate on determining the optimal scale for measuring the indirect area effect and to compare its effects on elevational diversity gradients relative to other potential drivers.

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References

- Able, K. P. and Noon, B. R. 1976. Avian community structure along elevational gradients in northeastern United-States. – *Oecologia* 26: 275–294.
- Arrhenius, O. 1921. Species and area. – *J. Ecol.* 9: 95–99.
- Bachman, S. et al. 2004. Elevational gradients, area and tropical island diversity: an example from the palms of New Guinea. – *Ecography* 27: 299–310.
- Beehler, B. 1981. Ecological structuring of forest bird communities in New Guinea. – *Monogr. Biol.* 42: 837–861.
- Brehm, G. et al. 2003. Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. – *Ecography* 26: 456–466.
- Brown, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. – *Global Ecol. Biogeogr.* 10: 101–109.
- Caley, M. J. and Schluter, D. 1997. The relationship between local and regional diversity. – *Ecology* 78: 70–80.
- Cardelus, C. L. et al. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. – *J. Ecol.* 94: 144–156.
- Colwell, R. K. and Hurr, G. C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. – *Am. Nat.* 144: 570–595.
- Colwell, R. K. et al. 2004. The mid-domain effect and species richness patterns: what have we learned so far? – *Am. Nat.* 163: E1–E23.
- Connor, E. F. and McCoy, E. D. 1979. Statistics and biology of the species-area relationship. – *Am. Nat.* 113: 791–833.
- Cornell, H. V. 1985. Local and regional richness of Cynipine gall wasps on California oaks. – *Ecology* 66: 1247–1260.
- Cornell, H. V. 1999. Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. – *Ecoscience* 6: 303–315.
- Cornell, H. V. and Lawton, J. H. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities – a theoretical perspective. – *J. Anim. Ecol.* 61: 1–12.

- Drakare, S. et al. 2006. The imprint of geographical, evolutionary and ecological context on species-area relationships. – *Ecol. Lett.* 9: 215–227.
- Dunn, R. R. et al. 2007. When does diversity fit null model predictions? Scale and range size mediate the mid-domain effect. – *Global Ecol. Biogeogr.* DOI: 10.1111/j.1466-8238.2006.00284.x.
- Evans, K. L. et al. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. – *Biol. Rev.* 80: 1–25.
- Graves, G. R. 1985. Elevational correlates of speciation and intraspecific geographic-variation in plumage in Andean forest birds. – *Auk* 102: 556–579.
- Graves, G. R. 1988. Linearity of geographic range and its possible effect on the population-structure of Andean birds. – *Auk* 105: 47–52.
- Graves, G. R. and Gotelli, N. J. 1983. Neotropical land-bridge avifaunas-new approaches to null hypotheses in biogeography. – *Oikos* 41: 322–333.
- Graves, G. R. and Rahbek, C. 2005. Source pool geometry and the assembly of continental avifaunas. – *Proc. Nat. Acad. Sci. USA* 102: 7871–7876.
- Grytnes, J. A. 2003. Species-richness patterns of vascular plants along seven altitudinal transects in Norway. – *Ecography* 26: 291–300.
- Grytnes, J. A. and Vetaas, O. R. 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. – *Am. Nat.* 159: 294–304.
- Gurevitch, J. and Hedges, L. V. 1999. Statistical issues in ecological meta-analyses. – *Ecology* 80: 1142–1149.
- Gurevitch, J. et al. 2001. Meta-analysis in ecology. – *Adv. Ecol. Res.* 32: 199–247.
- Hawkins, A. F. A. 1999. Altitudinal and latitudinal distribution of east Malagasy forest bird communities. – *J. Biogeogr.* 26: 447–458.
- He, F. L. et al. 2005. The local-regional relationship: Immigration, extinction, and scale. – *Ecology* 86: 360–365.
- Heaney, L. R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. – *Global Ecol. Biogeogr.* 10: 15–39.
- Herzog, S. K. et al. 2005. The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. – *Ecography* 28: 209–222.
- Hoffmann, M. H. et al. 2001. Phytogeographical analysis of plant communities along an altitudinal transect through the Kuraiskaya basin (Altai, Russia). – *Phytocoenologia* 31: 401–426.
- Holloway, J. D. 1987. Macrolepidoptera diversity in the Indo-Australian tropics—geographic, biotopic and taxonomic variations. – *Biol. J. Linn. Soc.* 30: 325–341.
- Kattan, G. H. and Franco, P. 2004. Bird diversity along elevational gradients in the Andes of Colombia: area and mass effects. – *Global Ecol. Biogeogr.* 13: 451–458.
- Kessler, M. 2000a. Altitudinal zonation of Andean cryptogam communities. – *J. Biogeogr.* 27: 275–282.
- Kessler, M. 2000b. Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. – *Plant Ecol.* 149: 181–193.
- Kessler, M. 2001. Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. – *Biodiv. Conserv.* 10: 1897–1921.
- Körner, C. 2000. Why are there global gradients in species richness? Mountains might hold the answer. – *Trends Ecol. Evol.* 15: 513–514.
- Kuper, W. et al. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. – *J. Biogeogr.* 31: 1477–1487.
- Lieberman, D. et al. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. – *J. Ecol.* 84: 137–152.
- Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. – *Global Ecol. Biogeogr.* 10: 3–13.
- MacArthur, R. H. 1972. *Geographical ecology*. – Harper and Row.
- McCain, C. M. 2005. Elevational gradients in diversity of small mammals. – *Ecology* 86: 366–372.
- McCain, C. M. 2006. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. – *Global Ecol. Biogeogr.* DOI: 10.1111/j.1466-822x.2006.00263.x.
- Md. Nor, S. 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. – *Global Ecol. Biogeogr.* 10: 41–62.
- Migliorini, M. and Bernini, F. 1999. Oribatid mite coenoses in the Nebrodi Mountains (northern Sicily). – *Pedobiologia* 43: 372–383.
- Mittelbach, G. G. et al. 2003. What is the observed relationship between species richness and productivity? Reply. – *Ecology* 84: 3390–3395.
- Patterson, B. D. et al. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. – *J. Biogeogr.* 25: 593–607.
- Rahbek, C. 1995. The elevational gradient of species richness – a uniform pattern. – *Ecography* 18: 200–205.
- Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. – *Am. Nat.* 149: 875–902.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. – *Ecol. Lett.* 8: 224–239.
- Ricklefs, R. E. 1987. Community diversity – relative roles of local and regional processes. – *Science* 235: 167–171.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. – Cambridge Univ. Press.
- Rosenzweig, M. L. and Ziv, Y. 1999. The echo pattern of species diversity: pattern and processes. – *Ecography* 22: 614–628.
- Samson, D. A. et al. 1997. Ant diversity and abundance along an elevational gradient in the Philippines. – *Biotropica* 29: 349–363.
- Sanchez-Cordero, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. – *Global Ecol. Biogeogr.* 10: 63–76.
- Sanders, N. J. 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. – *Ecography* 25: 25–32.

- Sanders, N. J. et al. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. – *Global Ecol. Biogeogr.* 12: 93–102
- Stevens, G. C. 1992. The elevational gradient in altitudinal range – an extension of Rapoport latitudinal rule to altitude. – *Am. Nat.* 140: 893–911.
- Storch, D. et al. 2005. The species-area-energy relationship. – *Ecol. Lett.* 8: 487–492.
- Stotz, D. F. 1998. Endemism and species turnover with elevation in montane avifaunas in the neotropics: implications for conservation. – In: Mace, G. M. et al. (eds), *Conservation in a changing world*. Cambridge Univ. Press, pp. 161–180.
- Terborgh, J. 1973. Notion of favorableness in plant ecology. – *Am. Nat.* 107: 481–501.
- Terborgh, J. 1977. Bird species-diversity on an Andean elevational gradient. – *Ecology* 58: 1007–1019.
- Terborgh, J. 1985. The role of ecotones in the distribution of Andean birds. – *Ecology* 66: 1237–1246.
- Terborgh, J. W. and Faaborg, J. 1980. Saturation of bird communities in the West-Indies. – *Am. Nat.* 116: 178–195.
- Whittaker, R. H. and Niering, W. A. 1975. Vegetation of Santa Catalina Mountains, Arizona. 5. Biomass, production, and diversity along elevation gradient. – *Ecology* 56: 771–790.

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