Ecology Letters, (2005) **8**: 224–239 doi: 10.1111/j.1461-0248.2004.00701.x

REVIEW

The role of spatial scale and the perception of large-scale species-richness patterns

Carsten Rahbek
Zoological Museum,
University of Copenhagen,
Universitetsparken 15, DK-2100
Copenhagen O, Denmark
Correspondence: E-mail:
crahbek@zmuc.ku.dk

Abstract

Despite two centuries of exploration, our understanding of factors determining the distribution of life on Earth is in many ways still in its infancy. Much of the disagreement about governing processes of variation in species richness may be the result of differences in our perception of species-richness patterns. Until recently, most studies of large-scale species-richness patterns assumed implicitly that patterns and mechanisms were scale invariant. Illustrated with examples and a quantitative analysis of published data on altitudinal gradients of species richness ($n = 204$), this review discusses how scale effects (extent and grain size) can influence our perception of patterns and processes. For example, a hump-shaped altitudinal species-richness pattern is the most typical (*c.* 50%), with a monotonic decreasing pattern (*c.* 25%) also frequently reported, but the relative distribution of patterns changes readily with spatial grain and extent. If we are to attribute relative impact to various factors influencing species richness and distribution and to decide at which point along a spatial and temporal continuum they act, we should not ask only how results vary as a function of scale but also search for consistent patterns in these scale effects. The review concludes with suggestions of potential routes for future analytical exploration of species-richness patterns.

Keywords

Altitudinal gradient, biogeography, grain size, latitudinal gradient, macroecology, predictive and null models, productivity gradient, spatial extent, spatial scale, species-richness pattern.

Ecology Letters (2005) 8: 224–239

INTRODUCTION

Biologists have been interested in large-scale patterns of species richness ever since the Europeans began their natural history explorations of the Earth in the 18th and 19th centuries (Ricklefs 2004). Recently, Brown & Maurer (1989) applied the term 'macroecology' to the study of these patterns. Macroecology involves characterizing and explaining statistical patterns based on large quantities of data. In describing what was new, Brown (1995) emphasized the 'statistical approach of macroecology' (p. 234) combined with 'searching for – and finding – patterns in data' (p. 232). Unfortunately, interpretation of this message resulted in a tendency to accept uncritically any data and view any scale of analysis as relevant and useful for any question, as long as the analysis was based on vast quantities of data and resulted in patterns and significant *P*-values (e.g. Blackburn & Gaston 1996a; see Gaston & Blackburn 1999 and Blackburn & Gaston 2002 for responses to the foregoing critique).

Brown (1995) himself clearly acknowledges the historical precedents of macroecology. Yet much of the arising macroecological literature, perceiving itself as a 'new discipline', first ignored only to regain later the already achieved wisdom in community and biogeographical ecology, for example 'how to differentiate between pattern generation and hypothesis testing' and 'why statistical significance and biological significance are not the same thing' (*sensu* Wiens 1989a; Rosenzweig 1995; Gotelli & Graves 1996). In ecology, the importance of scale in the resolution of geographical patterns of species richness has long been recognized (Hutchinson 1953; Whittaker 1977; Ricklefs 1987; Wiens *et al.* 1987; Wiens 1989a; Levin 1992; Schneider 1994). In contrast, until the late 1990s most large-scale studies of species-richness gradients tacitly assumed that patterns observed and mechanisms generating the patterns were similar at arbitrarily defined scales of analysis (Rahbek & Graves 2000; see also Rahbek & Graves 2001; Willis & Whittaker 2002). Only recently, despite the obvious

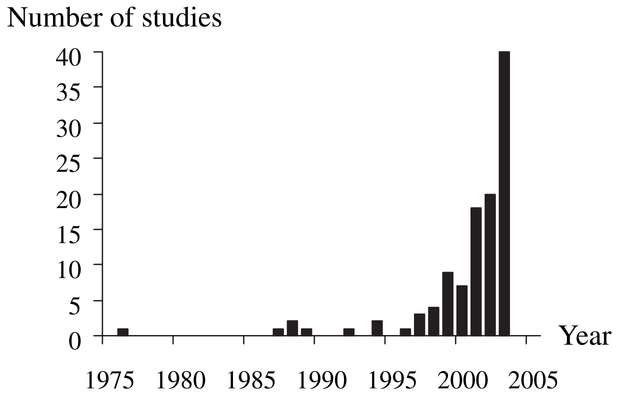

Figure 1 Publication trend of papers concerned *explicitly* with scale effects in patterns of species richness and/or analysis of patterns at multiple spatial scales. Data is compiled on the basis of examination of the literature found by searching the ISI Web of Science using 'species richness' or 'diversit*' and 'spati* scale*' as keywords.

macrofocus of large-scale studies of species distribution patterns, have scale issues become a focus of such studies (see Fig. 1 for a survey of the literature).

The definition and choice of scale can directly affect the results of any given analysis and the comparability of results between similar studies. Reconciliation of past and current disagreements regarding large-scale species-richness patterns may well depend on our understanding of scale effects. This is a prerequisite in the search for more refined theories of geographical variation in species richness. The lack of consensus regarding large-scale patterns of diversity, other than the latitudinal gradient of species richness, is not just a simple result of our current limitation in understanding the processes that generate them. It concerns elementary principles about how we standardize our basic description of patterns before even attempting to compare and explain them. A pattern is a statement about the relationship between several observations of nature suggesting a particular configuration of the properties of the system under examination (Wiens 1989a). It is not free of biases. Our perception of species-richness patterns is reflected in how we depict these graphically and statistically: 'Pattern, like beauty, is to some extent in the eye of the beholder' (Grant 1977 in Wiens 1989a).

In studies of geographical variation in species richness, two particularly interesting attributes of scale are the unit of sampling and the geographical space covered. The first attribute is defined by 'grain' and 'focus', grain being the size of the common analytical unit and focus, the area or inference space represented by each data point (Scheiner 2003). These attributes are also sometimes referred to by the somewhat more idiomatic 'scale of analysis' (Rahbek & Graves 2000). They all refer to the size of the individual sampling units defined by the inference space to which each datum applies (Wiens 1989b; Scheiner *et al.* 2000; Willig *et al.* 2003). The second attribute is 'extent', and refers to the inference space to which the entire set of sample units applies, describing the geographical space over which comparisons are made (Scheiner *et al.* 2000; Whittaker *et al.* 2001; Willig *et al.* 2003).

This review explores how scale of extent and grain size of studies may affect our conclusions regarding macroecological patterns based on species distributions. Pitfalls most common in macroecological studies associated with these scale effects are illustrated by new analyses of existing data sets in the literature. The general implication of scale effects on patterns of species richness is discussed with reference to a quantitative analysis based on the literature on altitudinal gradients of species richness (204 data sets from 140 studies). This focus on altitudinal gradients complements recent reviews focusing on latitudinal gradients that also include insightful discussion of scale issues (Willig *et al.* 2003; Hillebrand 2004). The latitudinal and altitudinal gradients have traditionally been viewed as mirrors of each other when obtained patterns are related to the general discussion of what causes spatial variation of species richness (MacArthur 1972; Brown 1988; Rohde 1992; Stevens 1992). This review will discuss how this perception of direct comparability relates to scale issues.

DOCUMENTATION AND PERCEPTION OF SPECIES-RICHNESS PATTERNS

Species richness is an elusive quantity to measure properly. Quantifying species richness without bias with respect to area and uneven sampling is by no means an easy task (see Rosenzweig 1995 and Gotelli & Colwell 2001 for thorough reviews). Failure to deal properly with these two factors in compared samples may result in patterns that are fundamentally different from the actual pattern of species richness (see Figures 1 and 2 in Rahbek 1995 for examples concerning the altitudinal gradients of species richness).

The classic latitudinal gradient of species richness is obviously not caused by latitude *per se*. The pattern is ultimately caused by historical, geographical, biotic, abiotic and stochastic forces (Willig *et al.* 2003). Latitude is a surrogate for one or more factors that relate to space and co-vary with latitude and are thought to directly influence species richness. However, while the use of surrogate variables in studies of large-scale patterns of species richness is widespread, it is also problematic. Latitudinal and altitudinal gradients represents surrogates for several environmental gradients that are often intercorrelated making tests of hypotheses associated with these gradients problematic and controversial (Willig *et al.* 2003).

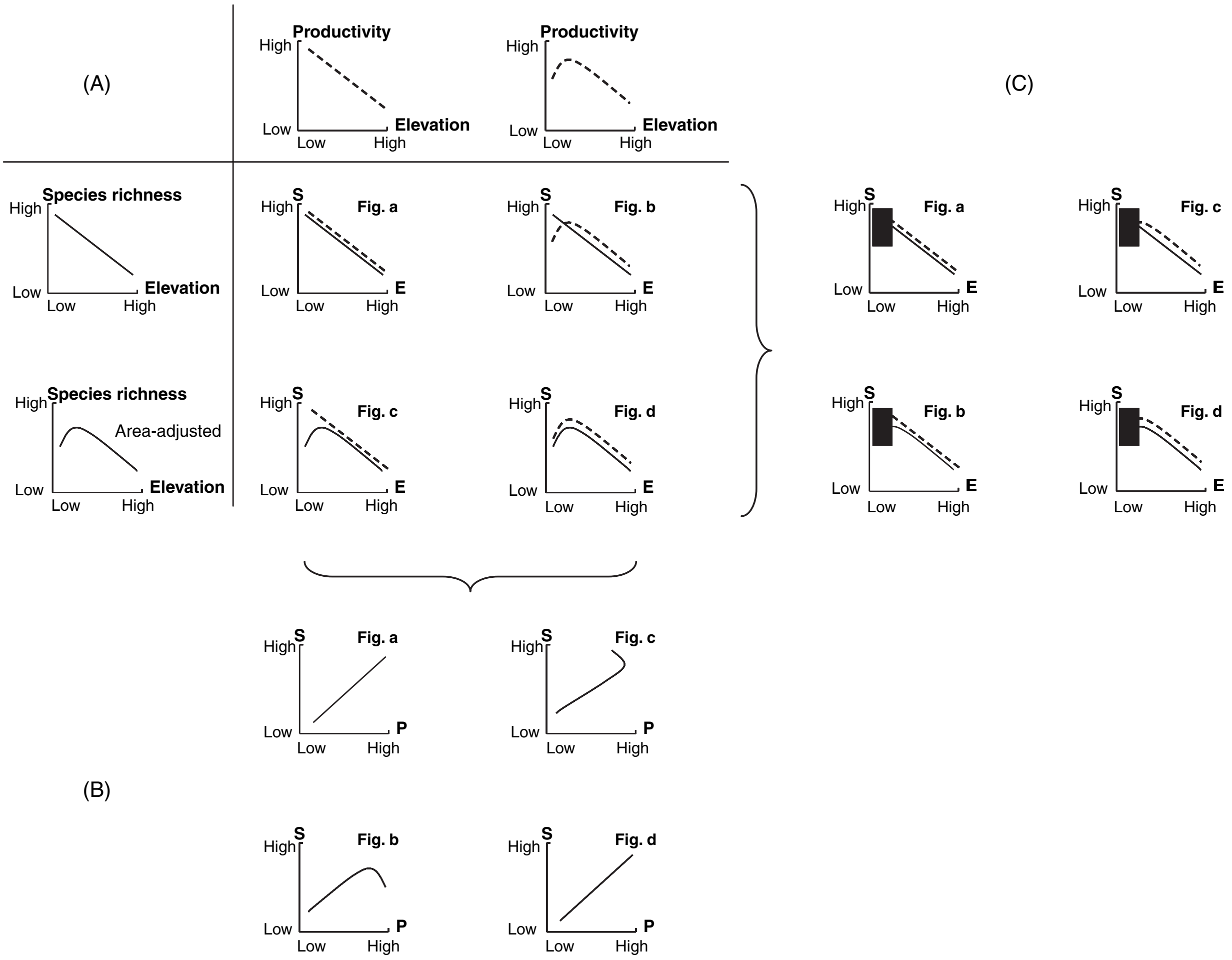

Figure 2 Relationship between productivity and species richness using elevation as a surrogate for productivity. (A) *Elevational species-richness (E-S) patterns*: left column shows an empirical case where the monotonic decline in species richness with increasing elevation transforms into a hump-shaped pattern if the elevational species–area relationship is used to standardize for variation in area among elevational zones. *Productivity-elevational (P-E) patterns*: upper row, left, classic view where productivity is believed to decrease from sea level to high altitudes; right, the case where productivity as a result of local climatic conditions peaks at intermediate elevations. *Overlaid E-S and P-E patterns*: (a) using an E-S gradient not adjusted for area and assuming a negative monotonic P-E relationship, the derived P-S pattern is a monotonic positive relationship; (b) using an E-S gradient adjusted for area and assuming a negative monotonic P-E relationship, the derived P-S pattern is hump-shaped; (c) using an E-S gradient not adjusted for area and assuming a hump-shaped P-E relationship, the derived P-S pattern is hump-shaped, i.e. the same as in (b); (d) using an E-S gradient adjusted for area and assuming a hump-shaped P-E relationship the derived P-S pattern is a monotonic positive relationship, i.e. the same as in (a). (B) Derived *productivity species-richness relationships*. (C) Perception of productivity species-richness pattern based on incomplete elevational gradients, i.e. missing data from lowest end of gradient (indicated by black boxes). (Based on case study including all 2801 breeding bird species of tropical biomes of South America; data from Rahbek 1997.)

For example, altitude has traditionally been viewed as a good surrogate for productivity because temperature decreases with altitude (MacArthur 1969; Orians 1969; Terborgh 1971). However, there is conflicting evidence indicating that productivity may sometimes peak at intermediate altitudes (Rahbek 1997; Kessler 2000). Nevertheless, patterns of altitudinal gradients of species richness, often assumed to simply mirror the latitudinal gradient, have frequently been cited as compelling evidence for various hypothesis associated with productivity, ambient energy and contemporary climate (Hutchinson 1959; MacArthur 1972; Wright 1983; Brown 1988; Stevens 1989, 1992; Currie 1991; Rosenzweig 1992, 1995; Abrams 1995; Whittaker *et al.* 2001). However, depending on how surrogacy is determined and whether or not sampling area is standardized, the same data can lead to directly contrasting patterns (Fig. 2A–C).

Incomplete sampling of environmental gradients, especially in conjunction with interpolation of species ranges, can directly bias the resulting pattern (Grytnes & Vetaas 2002; see also McCoy 1990). Shortening the extent of the altitudinal gradient by omitting the lower end can result in unidirectional bias and the appearance of a continuous decrease in species richness independent of the actual differences in the 'true' underlying pattern (Fig. 2C). Interestingly, in this case all four possible combinations of the two altitudinal and two productivity species-richness patterns depicted in Fig. 2 result in four identical patterns, each supporting the traditional idea of a monotonic relationship between species richness and productivity. Not surprisingly, altitudinal gradients of species richness have been interpreted in favour of both a monotonic and a hump-shaped relationship between productivity and species richness (e.g. Abrams 1995; Rosenzweig 1995).

ALTITUDINAL GRADIENTS OF SPECIES RICHNESS: ASSEMBLING THE PATTERNS

A search of the ISI Web of Science was performed on 29 July 2004 using the following search strings: ('elevatio*' or 'altitud*') and ('richness' or 'diversit*') and ('gradien*' or 'patter*' or 'transec*' or 'varian*'). The search was conducted using the option 'all document types' for the period 1995–2004 and included title, abstract and keywords. A total of 1227 papers were found. A closer examination of these papers provided 204 data sets from 140 papers (27 seemingly relevant papers of the 1227 could not be obtained). Multiple data sets are included from the same paper as separate entries if they concerned different taxonomic units (as identified by the author) or were collected from geographically separate mountain ranges or regions. In cases with multiple data sets reproduced from the same raw data, only the most standardized with regard to area and sampling effort is included. Not included are data sets that focus only on agricultural or disturbed habitat, endemic or restricted range size species, and those where transects are compiled from scattered data points more than 100 km apart.

The results are presented graphically, but not analysed formally in a meta-analysis (such as in Hillebrand 2004). The reason for this choice is that the reliability of such statistics depends strongly on the quality and comparability of the compared studies. The relatively short span of altitudinal gradients of species richness makes them particularly sensitive to effects of area, sampling regime, and/or effort (McCoy 1990; Rahbek 1995) as well as scale issues (this review). As Fig. 2 demonstrates, decisions concerning the analytical design of individual studies can completely turn around the statistical outcome related to the shape of the species-richness pattern. Given these issues, and as the aim here is to establish quantitative patterns to illustrate potential scale effects, the classification of the relationship between altitude and species-richness pattern is based on a visual examination of bivariate plots. Each data set is assigned to one of five patterns: monotonically decreasing; horizontal, then decreasing; hump-shaped; increasing; other. These categories and the approach are identical to the last quantitative review of the literature on altitudinal gradients of species richness covering publications prior to 1995 (Rahbek 1995). Each data set was additionally classified with respect to variables characterizing the taxonomic group as well as various aspects of scale related to grain and extent (details are given in the figure legends.

Generated statistical patterns are highly sensitive to the criteria for data extraction. To ensure that data gathering and interpretation were independent of my own perception, my colleague Dr Tom Romdal exclusively extracted the data from the literature. Additionally, all analyses were designed prior to and were independent of the data compilation.

SCALE EFFECTS: EXTENT

The extent of a geographical area or gradient sampled can have a pronounced impact on the derived pattern of species richness. While the pattern may be correct for a given sample, the result may also be scale sensitive. Figure 3A shows the quantitative distribution of various shapes of the altitudinal gradient of species richness. A hump-shaped species-richness pattern seems more typical than a monotonic decline (*c.* 50% and *c.* 25%, respectively, of all 204 studies), confirming previously published results (Rahbek 1995). Interestingly, while individual patterns may clearly be sensitive to area effects (e.g. Rahbek 1997; Bachman *et al.* 2004), sampling effort, and sampling of a shortened gradient missing sample points from low altitude, does not appear to change the overall distribution patterns of altitudinal gradients of species richness (Fig. 3A–D). However, a minimum requirement for any data set to elucidate variation over an environmental gradient is that it includes data spanning the entire gradient or at least the part of the gradient where changes in patterns are expected to occur. When considering the subsample of data sets fulfilling this requirement, the overall distribution of patterns does indeed change. The number of studies showing a monotonic decline in species richness decreases and the frequency of reported hump-shaped patterns approaches three of four studies (Fig. 3E and F). Again this result appears indifferent to standardization of area and sample effort, but notice that the individual pattern for vertebrates does changes as a result of these factors.

The relative distribution of different types of patterns does vary with the length of the gradient surveyed (Fig. 4A). At the smallest extent (sampled gradients ≤1000 m) a pattern of monotonic decrease in species richness is the most dominant shape. At all other size classes of extent, the hump-shaped pattern dominates (Fig. 4A). Again, this

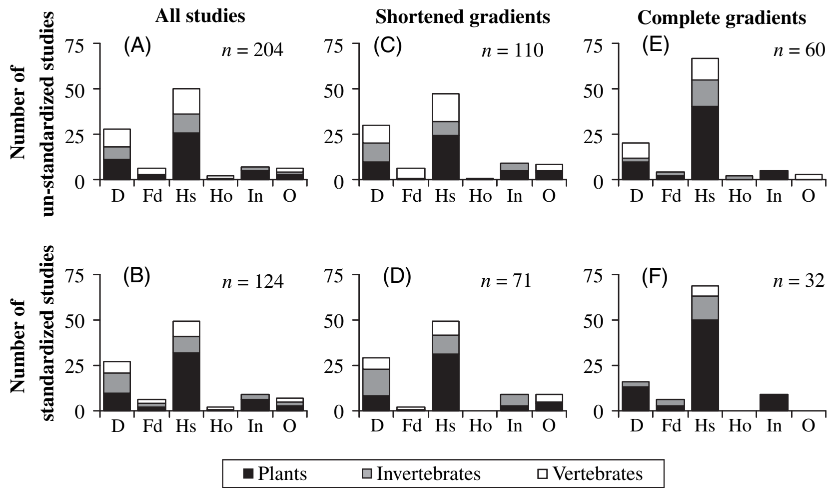

Figure 3 Percentage of published data sets showing various patterns of species richness and altitude: D, monotonically decreasing; Fd, flat-horizontal, then decreasing; Hs, hump-shaped; In, increasing; O, other. Top row includes all data sets (non-standardized). Bottom row includes only data sets judged to be standardized or with an attempt at standardization with regard to effect of area and sampling effort (standardized). Left column shows pattern for all studies, middle column only includes gradients with no data points below 500 m a.s.l. (shortened gradients), and right column only includes gradients with data points from ≤ 500 m to ≥ 2000 m a.s.l. (complete gradients).

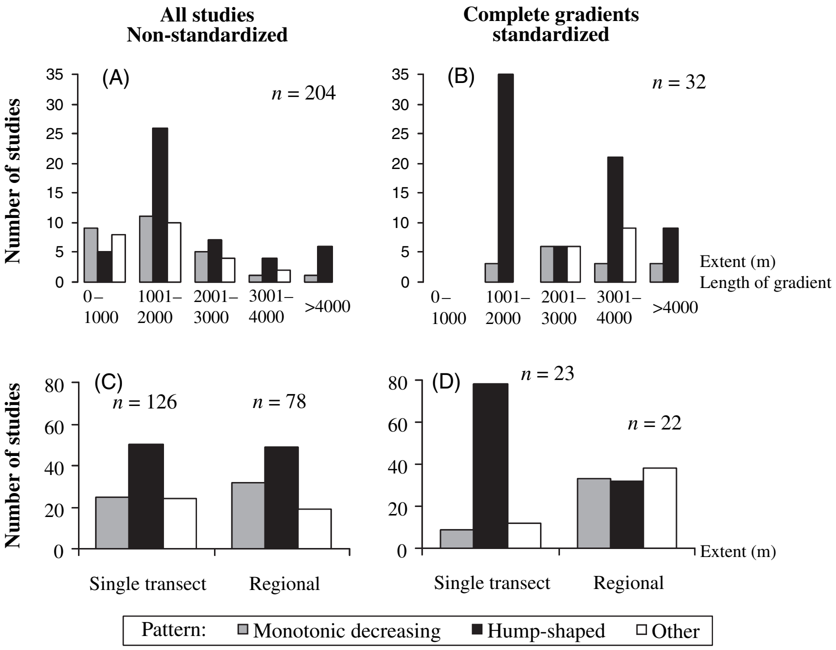

Figure 4 Percentage of published data sets showing various patterns of the relationship between altitude and species richness at various extents of scale grouped by 'length' of the gradient surveyed (top row) and whether data are sampled at a single, local transect or compiled at a broader regional scale (bottom row) for 'all studies – non-standardized' and 'complete gradients – standardized' respectively (see Fig. 3 for definitions).

pattern becomes even more pronounced when only 'complete' gradients standardized for area effects and sampling effort are considered (Fig. 4B). This increasing frequency of hump-shaped patterns for 'complete' gradients and with greater altitudinal extent is not paralleled when dividing the data sets into those obtained at a single, local, transect and those compiled at a larger regional scale (Fig. 4C and D). Considering all studies, a hump-shaped pattern typically emerges both at the local and regional extent. However, while this pattern becomes very pronounced when considering only 'complete' gradients standardized for area and sampling effort at the local scale, it disappears entirely at the regional scale.

The extent of latitudinal and altitudinal gradients

The hidden and implicit assumption in most of the literature dealing with both latitudinal and altitudinal species-richness gradients is that these gradients are scale invariant as far as mechanisms and processes determining variation in level of species richness are concerned. Results obtained at both gradients are thus viewed as directly comparable (MacArthur 1972; Brown 1988; Rohde 1992; Stevens 1992). This is, however, a dubious assumption because of the difference in extent of the two gradients (Rahbek 1997).

Complete latitudinal gradients span in excess of 10 000 km, whereas complete altitudinal (or depth) gradients rarely exceed a few kilometres, a difference of several orders of magnitude. As a consequence, the impact of historical and ecological mechanisms along the relatively short altitudinal gradients is likely to be different from those that operate along latitudinal gradients. Most species have a significantly larger distributional extent along latitudinal gradients than along altitudinal gradients. A greater range, *ceteris paribus*, increases the chance of allopatric speciation while reducing the risk of extinction (Rosenzweig 1992, 1995). For a species to persist within a given area there are lower limits to population size, as well as upper limits on population density.

Areas defined climatically by, for example, a fixed range of temperatures, are dramatically smaller along altitudinal gradients than latitudinal gradients. The conical shape of mountains means that the influence of altitude is compounded by one of area, and generally, area decreases rapidly with increasing altitude (MacArthur 1972; Lomolino 2001; Jones *et al.* 2003). However, in vast mountain ranges such as the Andes, altitudinal band areas are often narrowest at mid-altitude (Rahbek 1997). Many species particularly of vertebrates and vascular plants living in mountain habitats are probably incapable of maintaining viable populations within a single altitudinal band roughly characterized by uniform abiotic living conditions (approximate band widths of typically up to a few hundred metres). Thus, while the grain size of individual latitudinal band areas is unlikely to impose significant constraints on population viability *per se*, and thereby on the distribution of species, the size of climatically equivalent altitudinal bands most certainly does (Graves 1988). However, that is not to imply that the altitudinal and latitudinal range of a given species is straight forward correlated with altitudinal and latitudinal variation in climate in the same manner. In fact, bird species of the Andes with very narrow altitudinal range often have relatively extensive latitudinal ranges indicating a historical signature (speciation) in the distributions (Graves 1988).

Still the extremely short spatial extent of altitudinal gradients can potentially trigger a situation where species-richness patterns are significantly influenced by community-structuring factors such as source-sink population dynamics (Rahbek 1997; Kessler 2000; Lomolino 2001; Grytnes 2003a). In other words, modifying, biotic mechanisms are more likely to influence the altitudinal gradient of species richness than the pattern of species richness along the extensive latitudinal gradient (see Brehm *et al.* 2003 for a case study on geometrid moths along an Andean gradient). This difference may well be the reason for the lack of a uniform altitudinal pattern (Rahbek 1995; Grytnes 2003b; Fig. 3) as documented for latitude (Willig *et al.* 2003; Hillebrand 2004). This does not imply that the primary mechanisms influencing spatial variation of species richness along the two gradients cannot be the same.

SCALE EFFECTS: GRAIN

The choice of scale of analysis (i.e. grain size) directly influences our visual perception of spatial patterns of species as illustrated in Fig. 5A. Additionally, the use of too coarse a grain size results in an excessive loss of information and causes spurious extrapolation of high species densities in species-poor localities (Rahbek & Graves 2000; Fig. 5A). As Fig. 6 shows, the species-richness patterns for the altitudinal gradient vary with grain size. At the smallest grain-size (<0.1 km), hump-shaped patterns are relatively less frequent than when data is sampled using larger grain sizes (Fig. 6A). This may well be a sampling issue, as the hump-shaped pattern dominates when only considering ‘complete’ gradients standardized for area and sampling effort (Fig. 6B). Yet another distribution of shapes occurs when tabulating patterns in classes of width of altitudinal bands used to separate individual data points (Fig. 6C and D). Here hump-shaped patterns dominate at intermediate band size, especially when only considering ‘complete’ and standardized gradients, whereas a monotonic decreasing pattern is very rare.

Grain size and our view of determinants of species-richness patterns

Lyons & Willig (1999; see also Lyons & Willig 2002), in a recent analysis of species-richness patterns of South American bats and marsupials using nested quadrats of five sizes ranging in area from 1000 to 25 000 km, showed that the mechanisms believed to affect species richness are indeed scale sensitive. A subsequent analysis of species richness of South American hummingbirds at 10 spatial scales spanning two orders of magnitude (quadrat size *c.* 12 300–1 225 000 km^2) found that the perception of pattern and the conditional explanatory power of independent variables were directly dependent on the scale of analysis (i.e. grain size; Rahbek & Graves 2000, 2001). These findings were subsequently confirmed by other studies and seem to be general (e.g. van Rensburg *et al.* 2002; Blackburn *et al.* 2004).

At the continental extent, using ‘fine’ biogeographical grain sizes in contemporary climate-related models typically

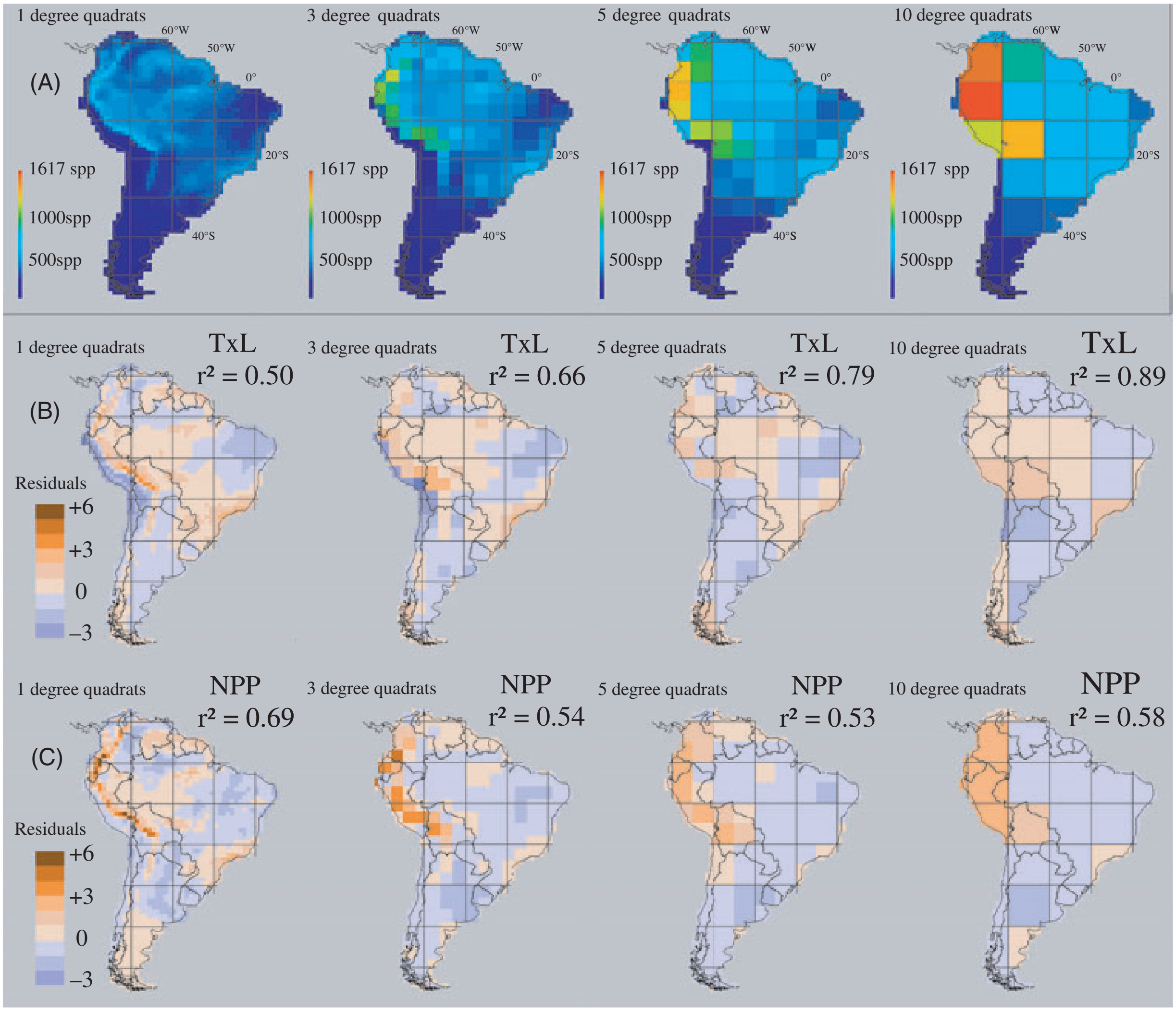

Figure 5 Effect of scale of analysis (grain size) on spatial variation in species richness and model residuals based on an analysis of 2869 breeding land and freshwater species of South American birds compiled at 1° × 1°, 3° × 3°, 5° × 5°, and 10° × 10°. (A) Spatial variation in species richness. (B) Spatial distribution of standardized residuals from a latitude × topographic relief model (L × T) comprising 'elevational range', 'latitude', and 'quadrat area' as variables (*cf.* Rahbek & Graves 2001). (C) Spatial distribution of standardized residuals from a net primary productivity model (NPP) comprising 'NPP', 'NPP^2' and 'quadrat area' (cf. Balmford *et al.* 2001) (re-analysed data from Rahbek & Graves 2001).

provides the strongest correlations for studies of species richness of all species (Currie 1991; Kerr *et al.* 2001; Jetz & Rahbek 2002; Hawkins *et al.* 2003; Ruggiero & Kitzberger 2004; Tognelli & Kelt 2004). However, the conditional explanatory power of other variables such as topography increases significantly with coarser grain size (Rahbek & Graves 2001). Plotting maps of the geographical distribution of model residuals based on the grain size and extent of the analysis often provides surprising insight that is otherwise lost in summary statistics (Rahbek & Graves 2001; Jetz & Rahbek 2002; Diniz-Filho *et al.* 2003; Tognelli & Kelt 2004). Models that explain less of the overall variation in species richness than contemporary climate models often yield far fewer large residuals (Rahbek & Graves 2001). This pattern remains scale invariant for various spatial grain sizes (Fig. 5B and C). Again, it is worth noting the disproportionate loss of information concerning the geographical distribution of positive and negative residuals with increasing scale of analysis.

The failure of contemporary climate and Net Primary Productivity (NPP) Model to conditionally explain the extraordinary abundance of species associated with humid tropical montane regions, the most species-rich biome on Earth, somewhat increases with scale of analysis (Fig. 5). The

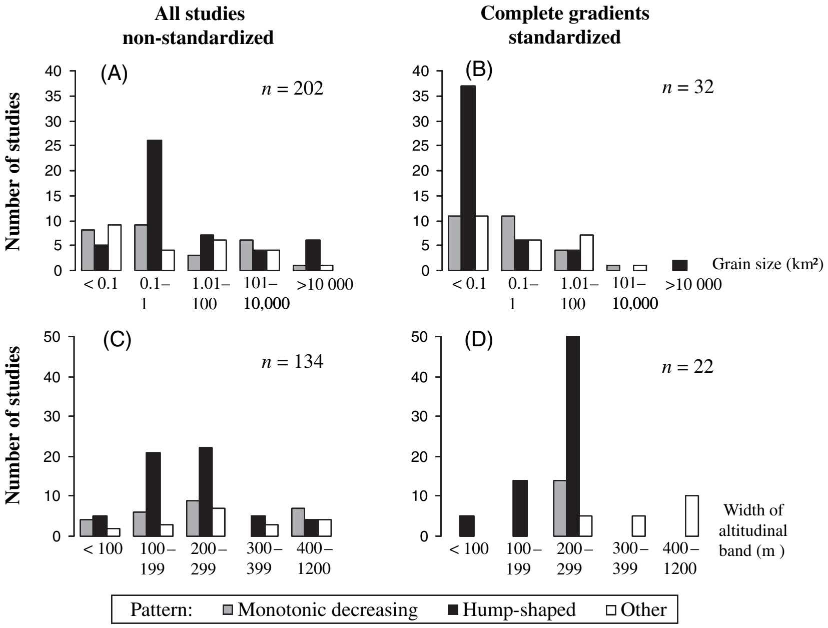

Figure 6 Percentage of published data sets showing various patterns of the relationship between altitude and species richness at various grain sizes grouped by 'grain size of sampling unit' (top row) or by the width of the altitudinal bands used to sample the gradient (bottom row) for 'all studies – non-standardized' and 'complete gradients – standardized', respectively (see Fig. 3 for definitions).

historical interaction between climate and topography, believed to be instrumental in generating the species pool from which local assemblages of species are drawn, becomes increasingly important at larger scale of analysis (Rahbek & Graves 2001). Clustering of narrow-ranging species into centres of endemism has typically been linked to historical explanations (Haffer 1969; Fjeldså *et al.* 1997; Jetz *et al.* 2004a). That the contemporary climate models, probably reflecting mechanisms of maintenance of species diversity (*cf.* Chesson 2000), often emerge as the most important predictor using 'fine' biogeographical grain sizes neatly fits the pattern related to the interaction between range sizes and the species richness. While a contemporary climate model may conditionally and effectively describe richness of the wide-ranging species, it may simultaneously fail to account for narrow-ranging species for which the significance of topography increases dramatically (Jetz & Rahbek 2002; but see Ruggiero & Kitzberger 2004 for somewhat mixed results), as it does with scale of analysis (Fig. 5).

Grain size and species range sizes

Patterns of species richness and species range size distributions are intertwined and interrelated (Hanski & Gyllenberg 1997) but also provide different approaches towards illuminating the causes of geographical variation in species assemblages and species densities. Patterns of frequency distribution of geographical range size have typically been described on the basis of the number of grid cells occupied. A substantial number of these studies have used extremely large grain sizes (e.g. 611 000 km^2) when illustrating the pattern of large spatial extents in, for example, the New World (e.g. Blackburn & Gaston 1996a,b). Other studies, typically covering a smaller spatial extent, characteristically

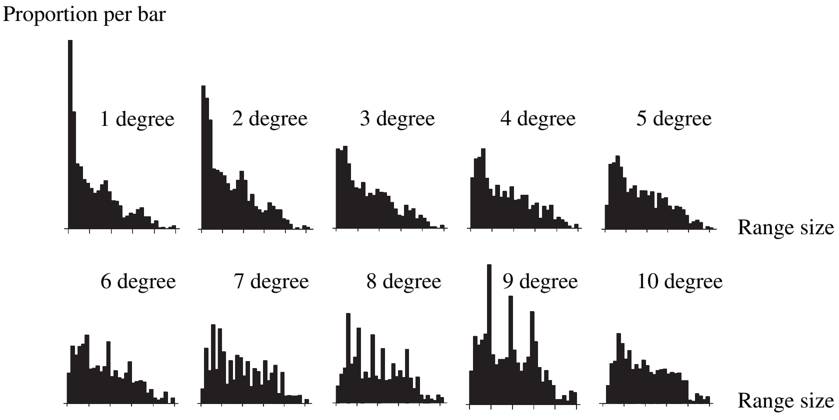

Figure 7 Effect of scale of analysis on the frequency distributions of range sizes for all breeding land and freshwater species of South American birds ($n = 2869$) compiled at 10 spatial grain sizes of latitudinal–longitudinal quadrats. X-axis for each scale comprises 30 equal-size bins that subdivide the scope of observed range sizes at that scale. Y-axis is the proportion of the sample in each bin. (Data from Rahbek & Graves 2001).

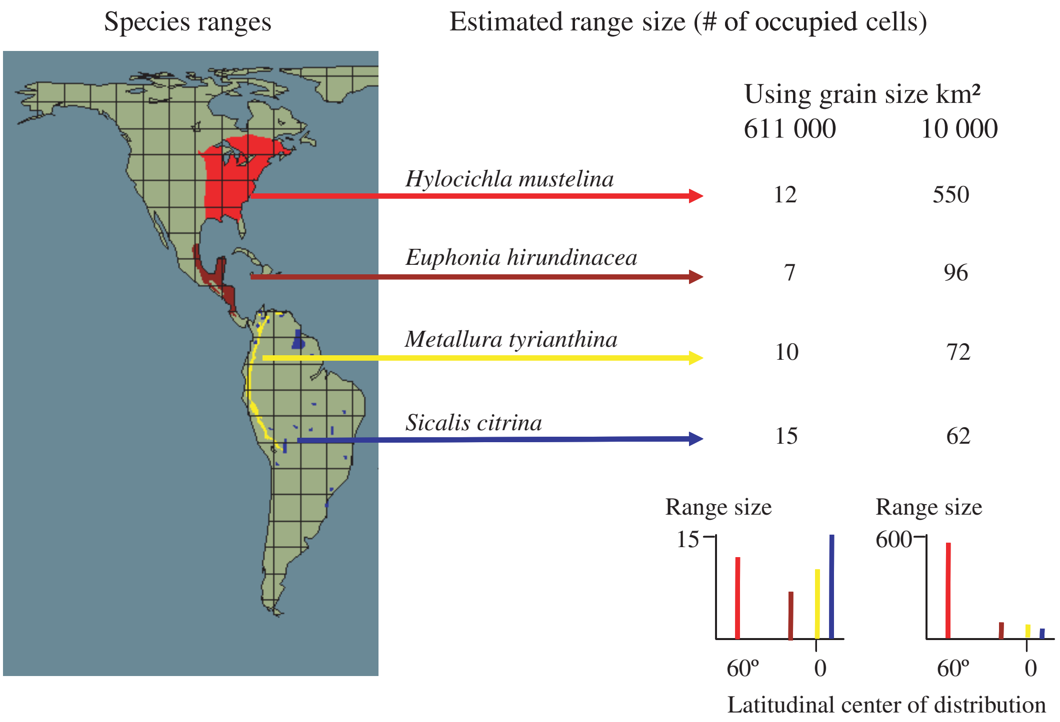

Figure 8 Effect of grain size on estimation of range sizes and geographical range-size patterns. The geographical distribution of four bird species is illustrated (left map), each representing typical distributions in different biogeographical areas of the New World and their estimated range size using quadrats of *c.* 611 000 and 10 000 km^2 (right two columns) respectively (see text for discussion). The two small histograms graphically illustrate how the perception of relative range sizes of the four species shifts with grain size. Consequently, a bias in perception of latitudinal range-size frequency distributions can result from use of inappropriate grain size.

use grain sizes several times smaller than 611 000 km^2 quadrats when measuring species range sizes, for example, 10 × 10 km grids for British birds (Gaston *et al.* 1998) or 50 × 50 km grids for European birds (Gregory *et al.* 1998).

Routinely, when discussing the general pattern of range-size frequency distribution from such an array of studies, the potential scale effect of extent is considered (Gaston & Blackburn 2000), while the scale effect of grain size is ignored. The tendency in the macroecological literature to ignore the effect of grain size is peculiar, given the obvious and enormous impact of this effect, especially because its direct influence on our perception of species occurrences *per se* is well described in the ecological literature (e.g. Levin 1992; Kunin 1998).

Range-size frequency distributions are not scale independent, but can vary significantly even when sampling the same distributions as a function of both grain size and species richness (Fig. 7; see also Figs 5 and 8). Grain size interacts with species distributions to produce different patterns at different scales. This in itself is not a bias. However, it certainly calls for caution when comparing data among studies conducted at different scale of analysis or when attempting to generalize from results of one study. In addition, mean, median and modal range size constitute an increasingly larger proportion of the total area of extent as grain size increases, indicating that the signal-to-noise ratio is inversely proportional to grain size (G.R. Graves and C. Rahbek unpublished data). The use of very coarse grain size to sample and describe geographical patterns of range size distributions may thus result in gross overgeneralizations (see also Fig. 8).

Grain size and geographical trends in bias

Generated patterns of species richness or range-size distributions using very coarse grain size are potentially influenced by geographical trends in bias, which comes in two forms: shape of range and apparent area of occurrence relative to grain size (i.e. the signal-to-noise ratio). This is especially true for the many species with relatively small or linear geographical ranges. Such species represent a significant proportion of taxa of the Neotropics in the New World, which in recent years has been used as one of the most common templates for macroecological studies of patterns of species richness and range size distributions (e.g. Lyons & Willig 1997, 1999, 2002; Willig & Lyons 1998; Gaston & Blackburn 2000; Rahbek & Graves 2000, 2001; Cardillo 2002; Husak & Husak 2003;

Koleff *et al.* 2003; Reed 2003; Blackburn *et al.* 2004; Olifiers *et al.* 2004; Rodriguero & Gorla 2004; Romdal *et al.* 2004; Ruggiero & Kitzberger 2004; Stevens 2004; Tognelli & Kelt 2004).

Data quality and geographical trends in bias associated with choice of grain size are ignored in much of the macroecological literature. This is perhaps the result of the 'macroecological approach' of analysing vast compilations of data (see also Gotelli & Graves 1996, pp. 308–309 for discussion of data quality). As exemplified below with New World birds, consideration of individual maps and their geographical properties is important to enable biologically meaningful conclusions based on generalized patterns from the overlay of multiple species distribution maps.

In the New World, the shape of birds' breeding ranges differs geographically, from the typically more rounded ranges of birds of North America (see maps in Price *et al.* 1995), and the more long and narrow range shapes of Central America (see maps in Howell & Webb 1995), to the long and altitudinally narrowly constrained distributions of most Andean species (see maps in Fjeldså & Krabbe 1990). While ranges of the vast majority of bird species appear to be continuous at larger geographical scales, the relatively few terrestrial species for which actual areas of occurrence are *extensively* dispersed within the extent of occurrence are mainly associated with tropical biomes. For example, the Stripe-tailed Yellow-finch (*Sicalis citrina* Pelzeln) is known from *c.* 60 localities of small habitat patches, where it is typically uncommon or rare (Fjeldså & Krabbe 1990) (Fig. 8). However, as the habitat of preference is sparsely distributed across South America, this species would occur in *c.* 15 different 611 000 km^2 grid cells, corresponding to *c.* 9 000 000 km^2, more than the distribution of the Wood Thrush [*Hylocichla mustelina* (Gmelin)], a common species across the entire eastern USA (Price *et al.* 1995; Fig. 8).

Geographical shapes of sampled areas, such as the isthmus of Central America when looking at New World patterns, introduce another source of geographical bias in overestimation of range sizes of species. Romdal *et al.* (2004) has recently demonstrated how different treatment of latitudinal band area influences the estimated peak and shape of the latitudinal gradient of species richness (see also McCoy & Connor 1980). Using a 611 000 km^2 grid cell template to estimate species range size distributions (e.g. Blackburn & Gaston 1996a), especially if combined with generalized distribution maps, may cause a gross overestimation of range sizes of many Central American birds (Fig. 8). Grid cells covering Central America contain relatively little land, compared with the average cells of North and South America. The Andes of western South America introduce the same kind of bias but are responsible for both a longitudinal trend in bias and a latitudinal one. While a significant fraction of Andean birds occurs in 3–6 grid cells of 611 000 km^2, their real range size is up to two magnitudes of area smaller! In fact, *c.* 700 (*c.* 25%) of the terrestrial breeding birds of South America have ranges <50 000 km^2. The number of such narrow-ranged species in Central America is 344 (*c.* 15%). In contrast, only three species with ranges <50 000 km^2 are confined to North America (Stattersfield *et al.* 1998).

In sum, statistical patterns based on the overlay of many distribution maps may be confounded – perhaps even caused – by trends in bias, and derived patterns may be geographically distorted. This risk increases with grain size (Fig. 5). Correlating other species attributes (e.g. weight and phylogenetic age) to a geographically biased pattern of species richness or range size distribution is relatively uninformative irrespective of formal statistical significance.

SCALE EFFECTS ARE ORGANISM SPECIFIC

An additional complication is that the influence of range size distribution on species richness patterns is related to the spatial scale or 'grain' at which different taxa perceive the environment, according to their body size (Ruggiero & Kitzberger 2004) and/or dispersal capabilities (Aukema 2004; Bailey *et al.* 2004; García & Ortiz-Pulido 2004). For example, an altitudinal gradient of 4 km is likely to be far more constrained to a species of bird than to a species of plant louse *relative* to the situation along a latitudinal gradient of thousands of kilometres. Consequently, while ecological and historical mechanistic processes may be very different for birds along an altitudinal gradient compared with a latitudinal gradient, the differences may be relatively less significant for a plant louse.

Intrataxonomic comparative studies of the altitudinal and latitudinal gradients obviously represent a convenient 'natural' system to investigate the effect of extent on mechanisms determining geographical variation in species richness. Nevertheless, this approach remains largely unexplored. An alternative approach is to conduct intertaxonomic comparisons along the same gradient, where scale is calibrated to reflect the different perceptions of scale from organism to organism. How to conduct taxon-specific scale calibration remains a challenge, and this has not yet been analytically explored in the context of large-scale patterns of species richness. Some recent studies have approached the question. In a meta-analysis of species–area relationships in benthos, Azovsky (2002) showed that the relationship between the number of benthos species and their size is spatially scale-dependent, stating that this was perhaps caused by size-dependent perception of environmental heterogeneity. Chust *et al.* (2003) adopted a multilevel approach in an attempt to identify landscape units from 'an insect perspective' based on the response of the insect assemblages to landscape heterogeneity (see also Chust *et al.* 2004).

THE CORRECT SCALE OF ANALYSIS IN MACROECOLOGY

There are no universal guidelines for deciding on the extent of scale and grain size when designing macroecological studies (but see Mayer & Cameron 2003). In studies that depend on derived figures from species distribution a rule of thumb could be to use a grain size as small as the smallest range sizes among the species within the study area. This rule assumes circular shaped distributions. A more conservative, but often impractical, rule would be 'as small as the smallest dimension of any range'. Alternatively, one should attempt to map individual species distributions as conservative areas of occurrence at the finest grain size permissible relative to the extent and knowledge of the species distribution within this – that is, with due consideration to the quality of records, by striking a balance between errors of omission and commission. The fulcrum of that balance would depend on the nature of the question asked. By using such a sampling protocol, one can always recompile data using a coarser grain size, or a smaller extent (within the domain sampled), adjusting to the scope judge relevant for the question attempted answered. Ideally, the scale of analysis (extent and/or grain size) can be varied systematically from the original scale to coarser scales in order to obtain the optimal resolution of pattern for a given analysis (Rahbek & Graves 2000).

Although resampling of data through the simple subdivision of space or translating overgeneralized 'blob' ranges depicted in tiny maps in commercial field guides using a fine grain size is tempting, it should be avoided for obvious reasons (Fig. 8). The use of such data leads to distortion of the pattern, increases sample size without a concomitant increase in primary information while artificially enhancing the degree of autocorrelation – and dramatically inflates the risk of a type I error.

SCALE EFFECTS AND LARGE-SCALE PATTERNS OF SPECIES RICHNESS

Refining the previous frame of 'local' vs. 'regional' patterns and processes (e.g. Ricklefs & Schluter 1993) to an interest in scale as a functional, continuous parameter will enhance our understanding of the effects of scale. The insight to be gained may reconcile some of the enduring controversies. For example, the extensively debated productivity species-richness pattern (steadily increasing or hump-shaped) is perhaps a result of scale effects among the compared studies (Waide *et al.* 1999; Purvis & Hector 2000; Chase & Leibold 2002; Scheiner & Jones 2002; Mittelbach *et al.* 2003; Whittaker & Heegaard 2003). The heated dispute on history and geography vs. contemporary processes has provoked a schism between historical and ecological approaches to diversity patterns (Ricklefs 2004), which seems to arise in part because of differences in the perception of spatial and temporal scale guiding decisions with respect to spatial framework design and subsequent data analyses. The schism exists despite the widespread consensus that a general theory of species diversity patterns must encompass spatial as well as temporal variation in patterns (Rohde 1992; Whittaker *et al.* 2001; Willig *et al.* 2003; Ricklefs 2004). It is most plausible that spatial species-richness patterns may have both contemporary ecological and historical evolutionary origins, origins that are not mutually exclusive (Ricklefs 2004; see Svenning 2003 for a nice case study). Of course, ecological studies should be conducted at scales appropriate to the local processes, namely, very fine, whereas historical studies might be conducted at scales that emphasize regional rather than local patterns. Intertwined with these deterministic processes are the impacts of stochastic effects that may occur, both in contemporary as well as historical space. Willig & Lyons (1998), for example, demonstrated this by extending the geometric constraints hypothesis (a null model) to environmental and geographical gradients space (see Gotelli 2001 and Colwell *et al.* 2004 for discussion of null models in macroecology). Essentially, it is meaningless to devise tests that would reject one or the other explanation, or to evaluate new ideas on this basis (Colwell *et al.* 2004; Ricklefs 2004).

The large-scale organization of diversity seems to represent a balance between local and regional processes, with relative dominance dependent on spatial grain size (Rahbek & Graves 2001). The general shape of the latitudinal gradient of species richness is a monotonic decrease in species richness towards the poles (Willig *et al.* 2003; Hillebrand 2004). It is almost universally found across taxa and habitats/biomes and appears to be scale invariant. However, even this pattern contains strong scale dependency, as parameters associated with the relationship between latitude and species richness changes with scale (literature summarized by Willig *et al.* 2003). The most pronounced scale effect is a strong dichotomy in latitudinal gradients between small local and large regional grains with regional scales producing much stronger and steeper gradients (Hillebrand 2004). In comparison, the altitudinal pattern found at local transects is the most clear cut of all those depicted in Figs 3, 4 and 6. Approximately 80% of the studies show a hump-shaped pattern (Fig. 4D). At the regional scale, this pattern changes entirely and is no more common than a monotonic decrease in species richness (Fig. 4D). Thus, perhaps as a consequence of the short scale of extent, the altitudinal pattern seems not to have a universal shape as does the latitudinal gradient (Figs 3, 4 and 6).

Altitudinal gradients as a suitable model to study scale effects

As a result of this scale sensitivity, altitudinal gradients appear to be an excellent choice to study the effects of scale on patterns of species richness. Additionally, altitudinal gradients are highly suitable for the study of contemporary climate, history and stochastic factors, as these vary along the altitudinal gradient itself and with the geographical (latitudinal) position of the gradient. This highlights the need for comparative studies, although they remain few and very recent (e.g. Grytnes 2003b).

Undoubtedly, scale effects in patterns of species richness are associated with underlying and intertwined gradients in alpha, beta and perhaps gamma diversity (Willig *et al.* 2003; Rodríguez & Arita 2004). Measurement of these units is influenced by area and sampling effort, which in principle can be fairly well controlled (or their effect explored) at well-executed field studies along altitudinal gradients. Hence, it is surprising that only about half of the included studies on altitudinal gradients attempt to deal with these two factors (Fig. 3A and B). The number of 'complete' and 'standardized' gradients is likewise astonishingly small (only 32 of 204; Fig. 3F).

Quantitative approaches as used here to elucidate patterns, potentially combined with the use of more explicit meta-analysis statistics (e.g. Hillebrand 2004), seem suitable to provide a rough overview of patterns in the results of published studies. Sadly, no factorial meta-analysis technique is currently available (Hillebrand 2004). As variables characterizing attributes of organisms, their environment and scale are intercorrelated (Figs 3, 4 and 6), caution is highly warranted when interpreting statistical results based on meta-analysis. Again, comparative field studies of altitudinal gradients seem a promising approach to help identify the details of possible consistent pattern in scale effects.

OUTLOOK

Traditional evaluation of hypotheses in large-scale, non-experimental, macroecological studies typically depends on deviations from a statistical null hypothesis. The results of these evaluations are usually expressed in terms such as r^2, r, F, CV, slope and P-values. It should be recognized that these values are scale sensitive and conditional on model design (Palmer 1994; Willig & Lyons 1998; Rahbek & Graves 2001; Lichstein *et al.* 2002; Lyons & Willig 2002; van Rensburg *et al.* 2002; Diniz-Filho *et al.* 2003; see Cressie 1993 for additional statistical insight). This is a problem as increased consistency in model evaluation is desirable to provide a more robust platform for identifying areas of disagreement among 'competing' hypotheses. Another major obstacle is autocorrelation. Spatial autocorrelation is an inherent quality of biogeographical data (Rahbek & Graves 2000; Pimm & Brown 2004). It is also an effect that is often correlated with sample size. However, the non-independency among data points violates basic assumptions of standard regression models and affects P-values and values of model parameters as well as model selection in stepwise procedures (Cressie 1993; Lichstein *et al.* 2002; Diniz-Filho *et al.* 2003; Tognelli & Kelt 2004). This makes comparison of such studies difficult.

In recent years, these issues have become increasingly recognized, but a clear way forward is yet to emerge. Below I offer suggestions of potential routes for future analytical exploration of data concerning large-scale species-richness patterns:

(1) We need to learn more about how scale affects patterns, for example by:
    (i) resampling empirical data at various scales of analysis to then explore the interrelationship among causal factors across scale (Rahbek & Graves 2001; Lyons & Willig 2002; van Rensburg *et al.* 2002; Blackburn *et al.* 2004);
    (ii) using computer simulations to conduct sensitivity analyses of patterns to scale of extent and grain size given various shapes of geographical domains, range size distribution frequencies, degree of coherency/patchiness in species distributions, etc. (e.g. Shen *et al.* 2004);
    (iii) conducting comparative field studies among geographically distinct but otherwise comparable gradients (e.g. Grytnes 2003b);
    (iv) conducting intrataxonomic comparative studies along the same gradient (e.g. Kessler 2000).

(2) We should abandon the use of traditional correlation/regression tests to evaluate hypothesis through rejecting of statistical null hypothesis and avoid using P-values from such test to evaluate and rank individual models (see, e.g. Manly 1997; Burnham & Anderson 2002).

(3) We should instead use spatial regression models wherever relevant (see Jetz & Rahbek 2002; Jetz *et al.* 2004a; Tognelli & Kelt 2004 for empirical examples).

(4) We should also explore patterns using null models and predictive models (Pimm & Brown 2004). Null models predict the effects in the *absence* of climatic and/or historical gradients (Colwell *et al.* 2004), whereas predictive models predict effects in the *presence* of mechanisms of interest (e.g. Allen *et al.* 2002; Rangel & Diniz-Filho 2004). Both types of models provide predictions in terms of the expected number of species to be compared with the observed number of species. Such data can be evaluated using traditional correlation tests and P-values if the predictions take into account geographical differences in the range-size frequency

distribution of assemblages of species and the signature of autocorrelation in the data.

(5) We should differentiate between local and global approaches to spatial data analysis in ecology (Jetz *et al.* 2004b).

(6) Above all, we should avoid prejudgment regarding new ideas and be open to new approaches, including those deriving from other disciplines. For example, geographically weighted regression techniques (Fotheringham *et al.* 2002), recently introduced by Foody (2004a) into macroecology from geography, seem to be an interesting supplement to spatial regression models. In particular, they may be a promising tool to elucidate local performance of predictor variables and to explore spatial non-stationarity and how that can give rise to varying trends in scale dependence trends (Foody 2004b; Jetz *et al.* 2004b). Note that this technique deals differently with autocorrelation compared with spatial regression techniques (Fotheringham *et al.* 2002) – an issue that needs to be explored further (Foody 2004b).

Finally, it is necessary to consider how results vary as a function of scale in order to put our knowledge regarding patterns and processes into perspective. Obviously, this is a necessary step, albeit only the initial one rather than the final goal. In addition to asking how our results vary as a function of scale, we should begin to search for consistent patterns in these scale effects (Wiens 1989b). If we are to relate patterns of diversity to scale in a way that elucidates the underlying processes we will need to know more about the biological underpinnings of variation in range size and ecological specialization, as well as the role of geographical heterogeneity in generating regional species richness. Combining sound statistical approaches with firm natural history knowledge and knowledge about biological processes will, eventually, enable us to attribute relative impact to various factors and to decide at which point along a spatial and temporal continuum they act.

ACKNOWLEDGEMENTS

For comments on drafts I would like to thank Robert K. Colwell, Gary R. Graves, John-Arvid Grytnes, Helmut Hillebrand, Michael Kessler, Christy M. McCain, Tom S. Romdal, Kasper Thorup, and Michael Willig. I am also grateful for the constructive comments by two anonymous reviewers and the subject editor Boris Worm. I would especially like to thank Gary R. Graves for discussions throughout the years on these issues and Tom Romdal for his critical contributions in compiling the data set for the quantitative analysis. Frank Wugt Larsen helped Tom in obtaining hardcopy versions of relevant papers. P. Williams kindly provided the WORLDMAP software used to manage the distributional data and to generate Figs 5 and 8. The macroecological research work was supported by the Danish National Science Foundation, grant J. no. 21-03-0221.

REFERENCES

Abrams, P.A. (1995). Monotonic or unimodal diversity-productivity gradients: what does competition theory predicts. *Ecology*, 76, 2019–2027.

Allen, A.P., Brown, J.P. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548.

Aukema, J.E. (2004). Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography*, 27, 137–144.

Azovsky, A.I. (2002). Size-dependent species-area relationships in benthos: is the world more diverse for microbes? *Ecography*, 25, 273–282.

Bachman, S., Baker, W.J., Brummitt, N., Dransfield, J. & Moat, J. (2004). Elevational gradients, area and tropical island diversity: an example from the palms of New Guinea. *Ecography*, 27, 299–310.

Bailey, S.A., Horner-Devine, M.C. & Luck, G., Moore, L.A., Carney, K.M., Anderson, S. *et al.* (2004). Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. *Ecography*, 27, 207–217.

Balmford, A., Moore, J., Brooks, T., Burgess, N., Hansen, L.A., Williams, P. *et al.* (2001). Conservation conflicts across Africa. *Science*, 291, 2616–2619.

Blackburn, T.M. & Gaston, K.J. (1996a). Spatial patterns in the geographic range sizes of bird species in the New World. *Phil. Trans. R. Soc. B*, 351, 897–912.

Blackburn, T.M. & Gaston, K.J. (1996b). Spatial patterns in the species richness of birds in the New World. *Ecography*, 19, 369–376.

Blackburn, T.M. & Gaston, K.J. (2002). Scale in macroecology. *Global Ecol. Biogeogr.*, 11, 185–189.

Blackburn, T.M., Jones, K.E., Cassey, P. & Losin, N. (2004). The influence of spatial resolution on macroecological patterns of range size variation: a case study using parrot, Aves: Psittaciformes, of the world. *J. Biogeogr.*, 31, 285–293.

Brehm, G., Sussenbach, D. & Fiedler, K. (2003). Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography*, 26, 456–466.

Brown, J.H. (1988). Species diversity. In: *Analytical Biogeography – An Integrated Approach to the Study of Animal and Plant Distribution* (eds Myers, A.A. & Giller, P.S.). Chapman and Hall, New York, NY, pp. 57–89.

Brown, J.H. (1995). *Macroecology*. The University of Chicago Press, London.

Brown, J.H. & Maurer, B.A. (1989). Macroecology – the division of food and space among species on continents. *Science*, 243, 1145–1150.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information–Theoretical Approach*. Springer-Verlag, New York, NY.

Cardillo, M. (2002). Body size and latitudinal gradients in regional diversity of New World birds. *Global Ecol. Biogeogr.*, 11, 59–65.

Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity-biodiversity relationship. *Nature*, 416, 427–430.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Chust, G., Pretus, J.L., Ducrot, D., Bedos, A. & Deharveng, L. (2003). Identification of landscape units from an insect perspective. *Ecography*, 26, 257–268.

Chust, G., Pretus, J.L., Ducrot, D. & Ventura, D. (2004). Scale dependency of insect assemblages in response to landscape pattern. *Lanscape Ecol.*, 19, 41–57.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004). The mid-domain effect and species richness patterns: What have we learned so far? *Am. Nat.*, 163, 0E1–E23.

Cressie, N.A.C. (1993). *Statistic for Spatial Data* (Revised edn). Wiley, Chichester, New York.

Currie, D.J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.*, 137, 27–49.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003). Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol. Biogeogr.*, 12, 53–64.

Fjeldså, J. & Krabbe, N. (1990). *Birds of the High Andes*. Zoological Museum, University of Copenhagen and Apollo Books, Svendborg, Denmark.

Fjeldså, J., Ehrlich, D., Lambin, E. & Prins, E. (1997). Are biodiversity "hotspots" correlated with current ecoclimatic stability? A pilot study using NOAA-AVHRR remote sensing data. *Biodiv. Conserv.*, 6, 401–422.

Foody, G.M. (2004a). Spatial nonstationarity and scale-dependency in the relationship between species richness and environmental determinants for the sub-Saharan endemic avifauna. *Global Ecol. Biogeogr.*, 13, 315–320.

Foody, G.M. (2004b). Clarifications on local and global data analysis. *Global Ecol. Biogeogr.*, in press.

Fotheringham, A.S., Brunsdon, C. & Charlton, M. (2002). *Geographically Weighted Regression: The Analysis of Spatially Varying Relationships*. Wiley, Chichester, Hoboken, NJ.

García, D. & Ortiz-Pulido, R. (2004). Patterns of resource tracking by avian frugivores at multiple spatial scales: two case studies on discordance among scales. *Ecography*, 27, 187–196.

Gaston, K.J. & Blackburn, T.M. (1999). A critique for macroecology. *Oikos*, 84, 353–368.

Gaston, K.J. & Blackburn, T.M. (2000). *Pattern and Process in Macroecology*. Blackwell Science Ltd, Oxford.

Gaston, K.J., Quinn, R.M., Blackburn, T.M. & Eversham, B.C. (1998). Species-range size distributions in Britain. *Ecography*, 21, 361–370.

Gotelli, N.J. (2001). Research frontiers in null model analysis. *Global Ecol. Biogeogr.*, 10, 337–343.

Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.*, 4, 379–391.

Gotelli, N.J. & Graves, G.R. (1996). *Null models in Ecology*. Smithsonian Institution Press, Washington, DC.

Graves, G.R. (1988). Linearity of geographic range and its possible effect on the population structure of Andean birds. *Auk*, 105, 47–52.

Gregory, R.D., Greenwood, J.J.D. & Hagemeijer, E.J.M. (1998). The EBCC atlas of European breeding birds: a contribution to science and conservation. *Biologia E Conservazione Della Fauna*, 102, 38–49.

Grytnes, J.A. (2003a). Ecological interpretations of the mid-domain effect. *Ecol. Lett.*, 6, 883–888.

Grytnes, J.A. (2003b). Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, 26, 291–300.

Grytnes, J.A. & 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.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science*, 165, 131–137.

Hanski, I. & Gyllenberg, M. (1997). Uniting two general patterns in the distribution of species. *Science*, 275, 387–400.

Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003). Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, 84, 1608–1623.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.*, 163, 192–211.

Howell, S.N.G. & Webb, S. (1995). *The Birds of Mexico and Northern Central America*. Oxford University Press, Oxford.

Husak, M.S. & Husak, A.L. (2003). Latitudinal patterns in range sizes of New World woodpeckers. *Southwest. Nat.*, 48, 61–69.

Hutchinson, G.E. (1953). The concept of pattern in ecology. *Proc. Natl Acad. Sci. USA*, 105, 1–12.

Hutchinson, G.E. (1959). Homage to Santa Rosalia, or "why are there so many kinds of animals?". *Am. Nat.*, 93, 145–159.

Jetz, W. & Rahbek, C. (2002). Geographic range size and determinants of avian species richness. *Science*, 297, 1548–1551.

Jetz, W., Rahbek, C. & Colwell, R.K. (2004a). Rarity, richness and the signature of history in centers or endemism. *Ecol. Lett.*, 7, 1180–1191.

Jetz, W., Rahbek, C. & Lichstein, J.W. (2004b). Local and global approaches to spatial data analysis in ecology. *Global Ecol. Biogeogr.*, in press.

Jones, J.I., Li, W. & Maberly, S.C. (2003). Area, altitude and aquatic plant diversity. *Ecography*, 26, 411–420.

Kerr, J.T., Southwood, T.R.E. & Cihlar, J. (2001). Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proc. Natl Acad. Sci. USA*, 98, 11365–11370.

Kessler, M. (2000). Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant Ecol.*, 149, 181–193.

Koleff, P., Lennon, J.J. & Gaston, K.J. (2003). Are there latitudinal gradients in species turnover?. *Global Ecol. Biogeogr.*, 12, 483–498.

Kunin, W.E. (1998). Extrapolating species abundance across spatial scales. *Science*, 281, 1513–1515.

Levin, S.A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943–1967.

Lichstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002). Spatial autocorrelation and autoregressive models in ecology. *Ecol. Monogr.*, 72, 445–463.

Lomolino, M.V. (2001). Elevation gradients of species-density: historical and prospective views. *Global Ecol. Biogeogr.*, 10, 3–13.

Lyons, S.K. & Willig, M.R. (1997). Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos*, 79, 568–580.

Lyons, S.K. & Willig, M.R. (1999). A hemispheric assessment of scale-dependence in latitudinal gradients of species richness. *Ecology*, 80, 2483–2491.

Lyons, S.K. & Willig, M.R. (2002). Species richness, latitude, and scale-sensitivity. *Ecology*, 83, 47–58.

MacArthur, R.H. (1969). Patterns of communities in the tropics. *Biol. J. Linn. Soc. Lond.*, 1, 19–30.

MacArthur, R.H. (1972). *Geographical Ecology*. Harper and Rowe Publishers, New York.

Manly, B.F.J. (1997). *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman and Hall, London.

Mayer, A.L. & Cameron, G.N. (2003). Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. *Landscape Urban Plan.*, 65, 201–217.

McCoy, E.D. (1990). The distribution of insects along elevational gradients. *Oikos*, 58, 313–322.

McCoy, E.D & Connor, E.F. (1980). Latitudinal gradients in the species diversity of North American mammals. *Evolution*, 34, 193–203.

Mittelbach, G.G., Scheiner, S.M. & Steiner, G.F. (2003). What is the observed relationship between species richness and productivity? Reply. *Ecology*, 84, 3390–3395.

Olifiers, N., Vieira, M.V. & Grelle, C.E.V. (2004). Geographic range and body size in Neotropical marsupials. *Global Ecol. Biogeogr.*, 13, 439–444.

Orians, G.H. (1969). The number of bird species in some tropical forests. *Ecology*, 50, 783–801.

Palmer, M.W. (1994). Variation in species richness: towards a unification of hypotheses. *Folia Geobot. Phytotaxon*, 29, 511–530.

Pimm, S.L. & Brown, J.H. (2004). Domains of diversity. *Science*, 304, 831–833.

Price, J., Droege, S. & Price, A. (1995). *The Summer Atlas of North American Birds*. Academy Press, San Diego, CA.

Purvis, A. & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405, 212–219.

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. & Graves, G.R. (2000). Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proc. R. Soc. Lond. B. Biol. Sci.*, 267, 2259–2265.

Rahbek, C. & Graves, G.R. (2001). Multiscale assessment of patterns of avian species richness. *Proc. Natl Acad. Sci. USA*, 98, 4534–4539.

Rangel, T.F.L.V.B. & Diniz-Filho, J.A. (2004). An evolutionary tolerance model explaining spatial patterns in species richness under environmental gradients and geometric constraints. *Ecography*, in press.

Reed, R.N. (2003). Interspecific patterns of species richness, geographic range size, and body size among New World venomous snakes. *Ecography*, 26, 107–117.

van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002). Species richness, environmental correlates, and spatial scale: a test using South African birds. *Am. Nat.*, 159, 566–577.

Ricklefs, R.E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235, 167–171.

Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.*, 7, 1–15.

Ricklefs, R.E. & Schluter, D., eds (1993). *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, IL.

Rodriguero, M.S. & Gorla, D.E. (2004). Latitudinal gradient in species richness of the New World Triatominae (Reduviidae). *Global Ecol. Biogeogr.*, 13, 75–84.

Rodríguez, P. & Arita, H.T. (2004). Beta diversity and latitude in North American mammals: testing the hypothesis of covariation. *Ecography*, 27, 547–556.

Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65, 514–527.

Romdal, T.S., Colwell, R.K. & Rahbek, C. (2004). The influence of band sum area, domain extent and range sizes on the latitudinal mid-domain effect. *Ecology*, in press.

Rosenzweig, M.L. (1992). Species diversity gradients: we know more and less than we thought. *J. Mamm.*, 73, 715–730.

Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, New York, NY.

Ruggiero, A. & Kitzberger, T. (2004). Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography*, 27, 401–416.

Scheiner, S.M. (2003). Six types of species-area curves. *Global Ecol. Biogeogr.*, 12, 441–447.

Scheiner, S.M. & Jones, S. (2002). Diversity, productivity and scale in Wisconsin vegetation. *Evol. Ecol. Res.*, 4, 1097–1117.

Scheiner, S.M., Cox, S.B., Willig, M.R., Mittlebach, G.G., Osenberg, C.W. & Kaspari, M. (2000). Species richness: scale effects and Simpson's paradox. *Evol. Ecol. Res.*, 2, 791–802.

Schneider, D.C. (1994). *Quantitative Ecology: Spatial and Temporal Scaling*. Academic Press, San Diego, CA.

Shen, W., Jenerette, G.D., Wu, J. & Gardner, R.H. (2004). Evaluating empirical scaling relations of pattern metrics with simulated landscapes. *Ecography*, 27, 459–469.

Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (1998). *Endemic Bird Areas of the World. Priorities for Biodiversity Conservation*. BirdLife International, Cambridge.

Stevens, G.C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.*, 133, 240–256.

Stevens, G.C. (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *Am. Nat.*, 140, 893–911.

Stevens, R.D. (2004). Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. *J. Biogeogr.*, 31, 665–674.

Svenning, J.C. (2003). Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecol. Lett.*, 6, 646–653.

Terborgh, J. (1971). Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology*, 52, 23–40.

Tognelli, M.F. & Kelt, D.A. (2004). Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography*, 27, 427–436.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I. *et al.* (1999). The relationship between productivity and species Richness. *Annu. Rev. Ecol. Syst.*, 130, 257–300.

Whittaker, R.H. (1977). Evolution of species diversity in land communities. *Evol. Biol.*, 10, 1–67.

Whittaker, R.J. & Heegaard, E. (2003). What is the observed relationship between species richness and productivity? Comment. *Ecology*, 84, 3384–3390.

Whittaker, R.J., Willis, K.J. & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *J. Biogeogr.*, 28, 453–470.

Wiens, J.A. (1989a). *The Ecology of Bird Communities: Foundations and Patterns*, Vol. 1. University Press, Cambridge.

Wiens, J.A. (1989b). Spatial scaling in ecology. *Funct. Ecol.*, 3, 385–397.

Wiens, J.A., Rotenberry, J.T. & Van Horne, B. (1987). Habitat occupancy patterns of North American shrubsteppe birds: the effect of spatial scale. *Oikos*, 48, 132–147.

Willig, M.R. & Lyons, S.K. (1998). An analytical model of latitude gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos*, 81, 93–98.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annu. Rev. Ecol. Evol. Syst.*, 34, 273–309.

Willis, K.J. & Whittaker, R.J. (2002). Species diversity-scale matters. *Science*, 295, 1245–1248.

Wright, D.H. (1983). Species-energy theory: an extension of species-area theory. *Oikos*, 41, 496–506.

Editor, Boris Worm
Manuscript received 30 April 2004
First decision made 24 June 2004
Second decision made 13 September 2004
Manuscript accepted 21 September 2004