



Spatial species-richness gradients across scales: a meta-analysis

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ABSTRACT

Aim We surveyed the empirical literature to determine how well six diversity hypotheses account for spatial patterns in species richness across varying scales of grain and extent.

Location Worldwide.

Methods We identified 393 analyses ('cases') in 297 publications meeting our criteria. These criteria included the requirement that more than one diversity hypothesis was tested for its relationship with species richness. We grouped variables representing the hypotheses into the following 'correlate types': climate/productivity, environmental heterogeneity, edaphics/nutrients, area, biotic interactions and dispersal/history (colonization limitation or other historical or evolutionary effect). For each case we determined the 'primary' variable: the one most strongly correlated with taxon richness. We defined 'primacy' as the proportion of cases in which each correlate type was represented by the primary variable, relative to the number of times it was studied. We tested for differences in both primacy and mean coefficient of determination of the primary variable between the hypotheses and between categories of five grouping variables: grain, extent, taxon (animal vs. plant), habitat medium (land vs. water) and insularity (insular vs. connected).

Results Climate/productivity had the highest overall primacy, and environmental heterogeneity and dispersal/history had the lowest. Primacy of climate/productivity was much higher in large-grain and large-extent studies than at smaller scales. It was also higher on land than in water, and much higher in connected systems than in insular ones. For other hypotheses, differences were less pronounced. Throughout, studies on plants and animals showed similar patterns. Coefficients of determination of the primary variables differed little between hypotheses and across the grouping variables, the strongest effects being low means in the smallest grain class and for edaphics/nutrients variables, and a higher mean for water than for land in connected systems but vice versa in insular systems. We highlight areas of data deficiency.

Main conclusions Our results support the notion that climate and productivity play an important role in determining species richness at large scales, particularly for non-insular, terrestrial habitats. At smaller extents and grain sizes, the primacy of the different types of correlates appears to differ little from null expectation. In our analysis, dispersal/history is rarely the best correlate of species richness, but this may reflect the difficulty of incorporating historical factors into regression models, and the collinearity between past and current climates. Our findings are consistent with the view that climate determines the capacity for species richness. However, its influence is less evident at smaller spatial scales, probably because (1) studies small in extent tend to sample little climatic range, and (2) at large

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grains some other influences on richness tend to vary mainly within the sampling unit.

Keywords

Area, climatic gradient, dispersal, diversity gradient, extent, grain, history, islands, latitudinal gradient, productivity.

INTRODUCTION

A major goal in biogeography and ecology is to understand the causes of taxonomic diversity gradients. Such gradients occur at spatial scales ranging in extent from a few metres (e.g. changes in species diversity along a lake shore; Nilsson & Wilson, 1991) to thousands of kilometres (e.g. the so-called latitudinal diversity gradient; Hillebrand, 2004). The nature, form and structure of data quantifying taxonomic diversity and its ecological or evolutionary correlates differ greatly between large and small scales, as do the methods used to measure them. As a result, research has often focused on one scale to the exclusion of others. However, the drivers of diversity and/or their relative influence may differ with scale (Whittaker *et al.*, 2003; Lavers & Field, 2006). Thus, a more complete understanding of diversity gradients and their causes requires study of their variation in relation to spatial scale.

A number of recent reviews have examined diversity gradients at different scales in relation to various factors, including latitude, climate, elevation, productivity and temperature (e.g. Waide *et al.*, 1999; Mittelbach *et al.*, 2001, 2007; Hawkins *et al.*, 2003a, 2007; Willig *et al.*, 2003; Hillebrand, 2004; Rahbek, 2005). Willig *et al.* (2003) and Hillebrand (2004) documented the generality of the latitudinal diversity gradient, and Hillebrand's meta-analysis found stronger and steeper latitudinal gradients at 'regional' than at 'local' scales. Waide *et al.* (1999) and Mittelbach *et al.* (2001) showed that the relationship between productivity and species richness tends to be hump-shaped at local scales and more monotonically positive at regional scales (see also Whittaker & Heegaard, 2003). Rahbek (2005) reviewed altitudinal gradients and found mainly hump-shaped altitude–richness relationships, but concluded that these relationships have less-consistent forms than latitude–richness relationships. At broad extents, Hawkins *et al.* (2003a) found strong energy–richness correlations, particularly outside the tropics, but Hawkins *et al.* (2007) found that the relationships between temperature and richness were inconsistent and highly variable across a wide range of scales and taxa.

The above studies illustrate the importance of looking at diversity gradients across spatial scales, but none provides a complete picture. Waide *et al.* (1999) and Mittelbach *et al.* (2001) considered only productivity as a potential driver of diversity, and Hawkins *et al.* (2007) considered only temperature. Hawkins *et al.* (2003a), Willig *et al.* (2003), Hillebrand (2004) and Mittelbach *et al.* (2007) did not consider diversity

gradients across small spatial extents. Rahbek (2005) focused on altitudinal gradients, and only at relatively small spatial extents. Clearly, diversity gradients must be studied across the full range of spatial scales and in relation to a variety of potential causal factors. In addition, it is important to concentrate on causal factors that have potential biological meaning. For example, latitude by itself cannot be a direct driver of diversity (Hawkins & Diniz-Filho, 2004); nor can altitude. Rather, diversity differences must relate to latitudinal or altitudinal covariates (e.g. energy, precipitation, species pool, time, area).

One review that did examine diversity gradients across a variety of spatial extents and sampling resolutions, and focused exclusively on biologically meaningful variables, was that by Wright *et al.* (1993). This short review covered 82 gradients and found energy to be by far the strongest correlate of richness. The correlation was stronger at larger grain sizes, but this was not the case for 'other factors'. In addition, correlations between richness and explanatory variables in general were much stronger for animals than for plants. Many additional diversity gradients have been documented since that study, and it is important to determine whether or not they support these intriguing findings.

In this study we used an extensive data base to evaluate how correlates of species-richness gradients vary with respect to spatial grain and extent, as well as with respect to taxon, system insularity and habitat medium. We classified the correlates of species richness ('explanatory' variables) into six categories based on the classifications of Fraser & Currie (1996) and Whittaker *et al.* (2001), modified slightly in the light of recent developments and the availability of data. We used our data base to test their relative ability to account for richness gradients statistically.

MATERIALS AND METHODS

The data base

The data base comprised non-experimental studies of richness gradients compiled by a National Center for Ecological Analysis and Synthesis (NCEAS) working group on species–energy theory. We searched journals, computerized literature data bases and data bases generated by other NCEAS working groups. The response variable of interest in any given study was richness (usually of species, but occasionally of genera or families) of any plant or animal group. A study was included if

we could extract coefficients of determination of ‘explanatory’ variables from any standard linear or nonlinear statistical technique. (We use the term ‘explanatory variable’ only in its statistical sense, without reference to any causality underlying correlations between richness and the environment.) A study was excluded if it considered only a single category of explanatory variable (see next section). Some studies included more than one richness variable; if these were sufficiently independent, they were included as separate ‘cases’. Care was taken to avoid pseudoreplication arising from separate studies analysing the same data. Where raw data could be extracted from the original paper, we recalculated the models to verify the published results, transforming variables if appropriate and computing coefficients of determination if the original authors did not. Therefore, the coefficients of determination sometimes differ from those originally reported.

Response, explanatory and grouping variables

We analysed two response variables: ‘primacy’ and ‘ r^2 ’. Both measure attributes of the single explanatory variable in each original study that, when modelled separately, accounted for the observed species-richness gradient better than any other measured variable. The relationship was usually linear, but in some cases it was quadratic or cubic. Following Hawkins *et al.* (2003a), we refer to this variable as the ‘primary’ variable, defined simply as the explanatory variable with the highest r^2 in the study. The response variable ‘ r^2 ’ was the coefficient of determination of that variable when modelled separately.

We define ‘primacy’ – the other response variable – as the proportion of times that a given correlate type (defined below) was the primary variable, relative to the number of times that the correlate type was analysed. Primacy therefore reflects two influences, both of which are important for an understanding of richness patterns globally: (1) the degree to which a given hypothesis among the six listed in Table 1 determines spatial variation in richness, and (2) the degree to which the independent variables measured in the studies summarized here operationalize the six hypothesized effects. In other words, primacy relates both to how strong the causal factors are, and to how they vary spatially. The first of the influences needs no elaboration. The second represents a complex interaction between how potential influences on richness vary across scales, coupled with methodological decisions by workers about the choice of variables to measure and how to measure them. It is also strongly affected by the amount of variation of each of the six hypothesized factors in the available studies. Although we cannot distinguish between the two statistically in this study, analysing primacy is an important step towards understanding the spatial variation in taxon richness globally.

We define the ‘correlate type’ as the broad hypothesis that the primary variable represents. Classification into correlate types was necessary because a very wide range of explanatory variables are measured in species-richness studies. We defined

six correlate types, based on Whittaker *et al.* (2001, table 3; see also Fraser & Currie, 1996), as follows.

- (1) Climate/productivity – variables describing the influence of climate, acting either directly through physiological effects, or indirectly through resource productivity or biomass. These two types of variable were combined because productivity variables are often modelled using climatic proxies, making it meaningless to distinguish them (Hawkins *et al.*, 2003a).
- (2) Environmental heterogeneity – measures of abiotic disturbance or spatial variation (within a sampling unit) in any variable, whether biotic or abiotic.
- (3) Edaphics/nutrients – variables describing soil, substrate or water quality.
- (4) Area – measures of the size of plots, habitats, islands or geographic regions. Note that this includes both direct sampling effects arising from plot sizes and indirect ecological and evolutionary effects arising from associations between area and habitat diversity or macroevolutionary processes.
- (5) Biotic interactions – any variable describing the direct or indirect effects of species in non-focal taxonomic groups, including the richness of other taxa but excluding variables measuring general food availability, which were classed under productivity.
- (6) Dispersal/history – variables capturing the effects of colonization limitation or other variables that are likely to contain a historical or evolutionary component. Although historical hypotheses are of considerable interest, very few studies matching our criteria for inclusion actually involve a measure of time; instead, most ascribed residual effects (such as differences between regions) to ‘history’.

In most cases, the assignment of variables to categories was obvious, but, in some, variables were assigned to non-obvious classes based on the judgment of the original authors about what the variable actually measured. Examples are given in Table 1. We tried to minimize the overlap between categories, but, because of the high collinearity of explanatory variables in richness studies, such overlap inevitably remains.

We also classified all the richness correlates in each study in the same way – not just the primary variables. This allowed us to calculate the primacy for each correlate type, based on the number of studies that included that type of correlate as a potential explanation of the species-richness gradient. This corrects for bias in the variables selected for inclusion in particular analyses. However, some bias could still arise if authors did not publish non-significant results. To control partially for such file-drawer effects, we excluded studies with only a single correlate type, because their inclusion would bias the representation of factors towards those favoured by individual authors; a study that tests only one correlate type (e.g. climate) is very likely to report a non-zero coefficient of determination. In short, studies are only included if at least one correlate type could be rejected as the primary one.

The response variables (primacy and r^2) were analysed with respect to correlate type and five grouping variables that could influence spatial diversity patterns. Two of these were grain and

Table 1 Classification scheme for predictor variables in richness studies. ‘Correlate type’ indicates the label we have attached to each category (abbreviation in brackets). ‘Measured variables’ lists (indicatively, not exhaustively) variables that are included in each class. Variables were sometimes assigned to classes based on claims made by the original authors.

Correlate type	Measured variables
Climate/productivity (C/P)	Rainfall, precipitation, maximum rainfall, summer rainfall, water deficit, actual evapotranspiration, productivity, plant biomass, total cover, normalized difference vegetation index (NDVI), accumulated respiration sum, potential evapotranspiration, air temperature, sea surface temperature, winter temperature, summer temperature, radiation, sunshine hours, temporal climatic variability.
Environmental heterogeneity (EH)	Habitat heterogeneity, number of microhabitats, landscape diversity index, biotope diversity, aspect diversity, patchiness, substrate heterogeneity, spatial climatic variability, topographic relief, altitudinal range, range in depth, forest fragmentation, abiotic disturbance, time since abiotic disturbance, Pfankuch stability index.
Edaphics/nutrients (E/N)	Bedrock type, soil structure, soil texture, measures of nutrient levels, organic matter content, nitrogen mineralization rate, soil water capacity, pH, summer pH, salinity, conductivity, water hardness, dissolved organic carbon, chemical oxygen demand, dissolved oxygen, water opacity, silicate concentration.
Area (A)	Region area, plot area, area above 2286 m, forest area, rain forest remnant area, woodland area, mountain area, habitat area, reserve area, shelter area, island area, archipelago area, lake area, drainage basin area, stream order, annual discharge, surface area, stream width, pond area, pool volume, shelf area, number of caves, gorge length.
Biotic interactions (B)	Competition, shading, grazing intensity, woody litter, number of trees > 150 years old, coral cover, sheep faecal density, vole disturbance, plant richness, tree species richness, herbaceous plant richness, phytoplankton richness, number of prey taxa, invertebrate richness, herbivore richness, fish richness.
Dispersal/history (D/H)	Biogeographic region, regional species richness, richness on nearest 25 km of mainland, patch connectivity, isolation, area of heathland within 2 km, distance to mainland, distance from Mindanao, distance from Carpathians, distance from Pyrenees.

extent, which are important facets of scale (Whittaker *et al.*, 2001). Grain is the size (e.g. geographical area) of the base unit of analysis, and is often the same or approximately the same as the focus, which is the size of the sampling unit (Dungan *et al.*, 2002). Geographic extent is the size of the entire study area. Scale dependence occurs when the form or parameterization of a relationship changes with grain/focus or extent (Willig *et al.*, 2003). The five grouping variables were as follows.

(1) Taxon – plants vs. animals. We expect differences in species-richness patterns and their correlates because of the fundamental trophic, physiological and mobility differences between plants and animals. In one case the focal taxon was mycorrhizal fungi, and in two cases lichens; we put each of these into the ‘plant’ class.

(2) Insularity – insular vs. connected. We expect insularity to affect richness patterns and their correlates (MacArthur & Wilson, 1967). Study systems were designated insular or connected on the basis of the habitat medium: insular systems were patches of land surrounded by water or patches of water surrounded by land. Thus, insular sites comprised true islands separated by water, ponds/lakes separated by land, or rivers in different drainage basins. Connected sites comprised contiguous grid cells or habitats, terrestrial habitat fragments in a terrestrial matrix, or ponds or rivers connected by waterways.

(3) Habitat medium – land vs. water. Differences in richness patterns and their correlates are expected because of fundamental differences in, among other things, the nature of the matrix supporting life and the availability of water (variable on land but not in water). Thus, terrestrial habitats were distinguished from freshwater/marine habitats.

(4) Grain – three levels of grain were distinguished: small (< 10 km²), medium (10–500 km²), and large (> 500 km²). This is expected to be important because the area of the

base unit defines the spatial scale of the study, and different grains capture different levels of spatial heterogeneity within units.

(5) Extent – four levels were distinguished based on the greatest linear geographical separation of sampling points: < 10 km, 10–100 km, 100–1000 km and > 1000 km. Extent captures inter-unit variation. The smallest extent is intended to represent ‘local’ diversity gradients, whereas the largest represents studies across major portions of continents, entire continents, and multiple continents. This factor is expected to be important because it defines the portion of the planet’s surface that was sampled, whereas the range in heterogeneity sampled within it determines whether the sample is representative and sufficient for describing and analysing relationships.

Cases that could not be unambiguously assigned to a category (e.g. studies spanning both land and water) were excluded from that specific analysis, so sample sizes vary slightly across analyses.

The data are publicly available via the NCEAS data repository: go to <http://knb.ecoinformatics.org/knb/style/skins/nceas/index.html> and then browse the data sets. The entry is called ‘Scale and richness gradients’ and has the ID ‘nceas.284.4’.

Statistical analysis

Analysis of primacy

Primacy is defined as the proportion of cases in which a given correlate type provided the highest r^2 when tested against one or more other correlate types. However, not all correlate types were tested in all studies, and their combinations also vary.

This affects the chance that a given correlate type appears as a primary variable, complicating the test of its statistical significance. We therefore developed a null model to establish the expectation of primacy under random variation of r^2 among correlate types and studies. We built a binary (0/1) matrix indicating when each correlate type was included in each study, and then replaced the '1' values by random r^2 values. From this, we calculated the null expectation of primacy for each correlate type, conditioned by the observed frequencies of tests in the real studies in the data set and the real combination of correlate types in the studies. This randomization procedure was conducted 1000 times. The primacy values obtained from the procedure can be interpreted as the primacy distribution for a given correlate type if its importance relative to the other correlate types tested was due to chance alone. Using the means and standard errors obtained from this null distribution, we compared the observed primacy of each correlate type with its null expectation using a *t*-test. We used the same approach to compare primacies with their null expectations within categories of the grouping variables (e.g. for plants and animals separately). Finally, we used standard errors from the null distributions in *t*-tests to compare the primacy of each correlate type between grouping-variable categories (e.g. primacy of area for plants compared with primacy of area for animals), applying a Bonferroni correction where there were more than two categories. The primacy results were qualitatively the same as those obtained by means of contingency table analysis (results not shown), which was conducted in S-Plus version 6, following Crawley (2002).

Analysis of coefficients of determination

Differences in the explanatory power of each correlate type across all data sets were tested using one-way analysis of variance (ANOVA). There is considerable variation in sample size among categories (results not shown), the main trend being that large-grain studies tend to have larger sample sizes. Furthermore, studies in terrestrial, non-insular systems tend to have larger sample sizes than others. Given this significant structure in the sample sizes, we analysed both adjusted r^2 (r^2_{adj}) and *z*-transformations of *r*-values, weighted by sample size (Hedges & Olkin, 1985). Here we report only the analysis of r^2_{adj} ; the other analysis gave no further insight. The adjustment of r^2 (standard method) takes into account both sample size and model complexity. Model complexity is nearly constant in our study because the coefficients of determination relate to single-variable models, with the explanatory variable only occasionally categorical or fitted nonlinearly. To determine whether or not the grouping variables influenced the ability of the six hypotheses collectively to account for variance in richness gradients, we used five one-way ANOVAs. The distributions of coefficients of determination were sufficiently normal and homoscedastic that transformation of the data was not required. We also conducted tentative two-way ANOVAs that compared the mean r^2_{adj} values of the correlate types

within categories of the grouping variables (e.g. for plants and animals separately), thus matching the primacy analyses described above. In addition, we performed two-way ANOVAs using all pair-wise combinations of the grouping variables in turn (e.g. grain and extent; insularity and taxon), and a six-way ANOVA using all the variables and a combination of non-automated forward and backward stepwise selection. All ANOVAs used Type III sums of squares. These analyses were tentative because of small sample sizes in some cases, and because of the number of comparative analyses being carried out, among other reasons. Accordingly, Bonferroni corrections were applied, and only the strongest results are considered worthy of attention. A relatively simple minimal adequate model was achieved (Crawley, 1993). In all the ANOVAs, the residuals were carefully checked for normality, homoscedasticity, leverage, etc. If these checks caused any doubt about the robustness of the ANOVA result, then that result was verified by means of nonparametric tests (Mann–Whitney *U*-tests and Kruskal–Wallis tests); in all cases the parametric ANOVA results were supported.

RESULTS

Structure of the species-richness data

We found 297 publications containing 393 analyses ('cases') meeting our criteria for inclusion. The cases covered a very wide range of taxa, habitats and scales, but, overall, studies of animal species richness were more common than studies of plant species richness (268 vs. 125), and insular habitats were less often studied than connected habitats (97 vs. 266). Studies of terrestrial habitats (259 cases) were better represented than studies of aquatic/marine habitats (124, of which 35 were exclusively marine and 85 exclusively freshwater). With respect to scale, more cases were small-grained (< 10 km²) than medium- or large-grained (210 vs. 77 vs. 106), even though studies of local extent were least common and continental/intercontinental most common (35 vs. 153).

We found under-representation of types of study, in various respects. First, the geographical distribution of study sites (Table 2) is strongly biased towards Europe and North America, with notably poor coverage in Asia (especially non-Palaeartic), South America and the oceans. Second, some combinations of correlate types are much more strongly represented in the literature than others (Table 3). For instance, edaphics/nutrients are commonly examined in combination with climate/productivity (137 cases) or environmental heterogeneity (108), but not with dispersal/history (19) or biotic interactions (34). Only 34 cases combine biotic interactions with dispersal/history. Third, Figs 1–3 and Table 4 show that tests of some correlate types are under-represented in the literature at certain scales or for particular types of study system. Most notably, few studies examined the effects of edaphics/nutrients or biotic interactions at large grains. Few cases correlate biotic interaction variables with plant richness (18 cases: only three are insular, two are < 10 km extent, and

Table 2 Number of cases in our data set from each region of the world listed.

Region	Number of cases
Africa	31
Asia	8
Atlantic	22
Australia/New Zealand	30
Central America/Caribbean	13
Cross region	11
Europe	94
Global	16
Indo-Pacific tropical islands	13
Mediterranean	9
North America	120
South America	19
Southern Ocean	7

Table 3 The distribution of analyses of combinations of correlate types. The values shown in the triangular grid represent the number of cases in which the two correlate types were tested against each other. See Table 1 for classification scheme.

Correlate type						Total number of cases including the correlate type
	C/P	EH	E/N	A	B	
C/P						280
EH	196					273
E/N	137	108				170
A	126	144	78			221
B	60	62	34	54		96
D/H	53	80	19	92	34	115

C/P, climate/productivity; EH, environmental heterogeneity; E/N, edaphics/nutrients; A, area; B, biotic interactions; D/H, dispersal/history.

only one includes marine data). Few studies test biotic interaction variables in aquatic/marine media (18 cases: three for plants, one is > 500 km² grain). For dispersal/history variables, only 27 cases use plants (mostly large extent), and only 22 are aquatic/marine (all are of animals, four are marine, one is < 10 km extent). Overall we found few suitable (observational) studies at < 10 km extent, including only two for insular systems (Table 4).

The average study tests 2.94 ± 0.045 (mean ± 1 SE) correlate types, according to our classification. This number varies little across correlate types, except for studies in which climate/productivity is primary. These studies have slightly fewer correlate types tested in the same study than do studies in which edaphics/nutrients, area or biotic interactions are primary (Table 5; Kruskal–Wallis test: $P < 0.001$, $n = 393$ cases). Table 5 also details the other correlate types that were tested when each type was primary. We used these data to create our null expectations for primacy (see Materials and Methods). Note that studies including climate often test a range of climate variables, which may increase its primacy. We

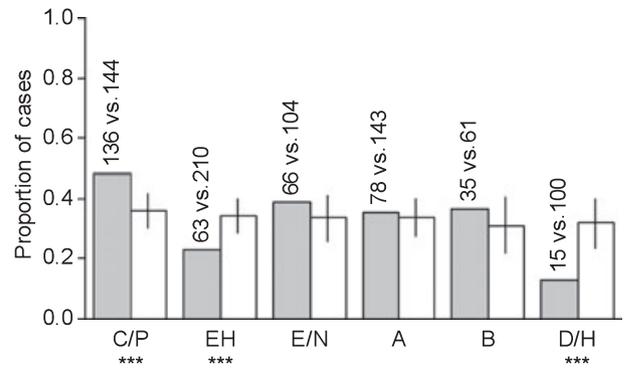


Figure 1 Primacy across the entire data base. All potential explanatory variables in each study were assigned to one of six correlate types (see Table 1 for further details: C/P, climate/productivity; EH, environmental heterogeneity; E/N, edaphics/nutrients; A, area; B, biotic interactions; D/H, dispersal/history). The shaded bars show the primacy of each correlate type (see Materials and Methods). The numbers above each bar represent the number of cases in which the correlate type was primary versus the number of cases in which it was tested but was not primary. The overall sample size is $n = 393$ cases in the data set. The asterisks under the axes show the significance of the primacy, compared with the null expectation: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; no asterisk, $P > 0.05$. The unshaded bars show the null expectations, with the 95% confidence intervals from 1000 randomizations.

found no trend through time in the number of correlate types tested per study (Spearman's rank $\rho = -0.009$, $P = 0.85$). Moreover, there was no change in mean r^2_{adj} over time (Spearman's rank $\rho = -0.003$, $P = 0.95$).

Which variables correlate best with species-richness gradients?

Across all the data sets, primacy differs strongly among the correlate types (Fig. 1). Climate/productivity is most often the best correlate of richness ('primary') when it is tested, despite the preponderance of small-grained (< 10 km²) studies in which the correlation is much weaker (Fig. 3a). It is primary in 49% of the studies in which it was tested (i.e., primacy = 49%). This is significantly higher than the null expectation of 36%, based on simulation (Fig. 1). In contrast, the primacy of environmental heterogeneity and historical factors is only 23% and 13%, respectively, in both cases significantly lower than the null expectations.

However, primacy differs among categories of most of our grouping variables (Figs 2 & 3), suggesting important biotic, abiotic and scale effects on the main drivers of species-richness gradients. These effects were strongest on the primacy of climate/productivity. We now go through the grouping variables in turn. Taxon had a minimal effect on primacy (Fig. 2a): no correlate type had significantly different primacy between animals and plants. In contrast, for connected systems, the primacy of climate/productivity was much higher, that of heterogeneity slightly higher, and that of area and biotic interactions lower than for insular systems (Fig. 2b). Climate/

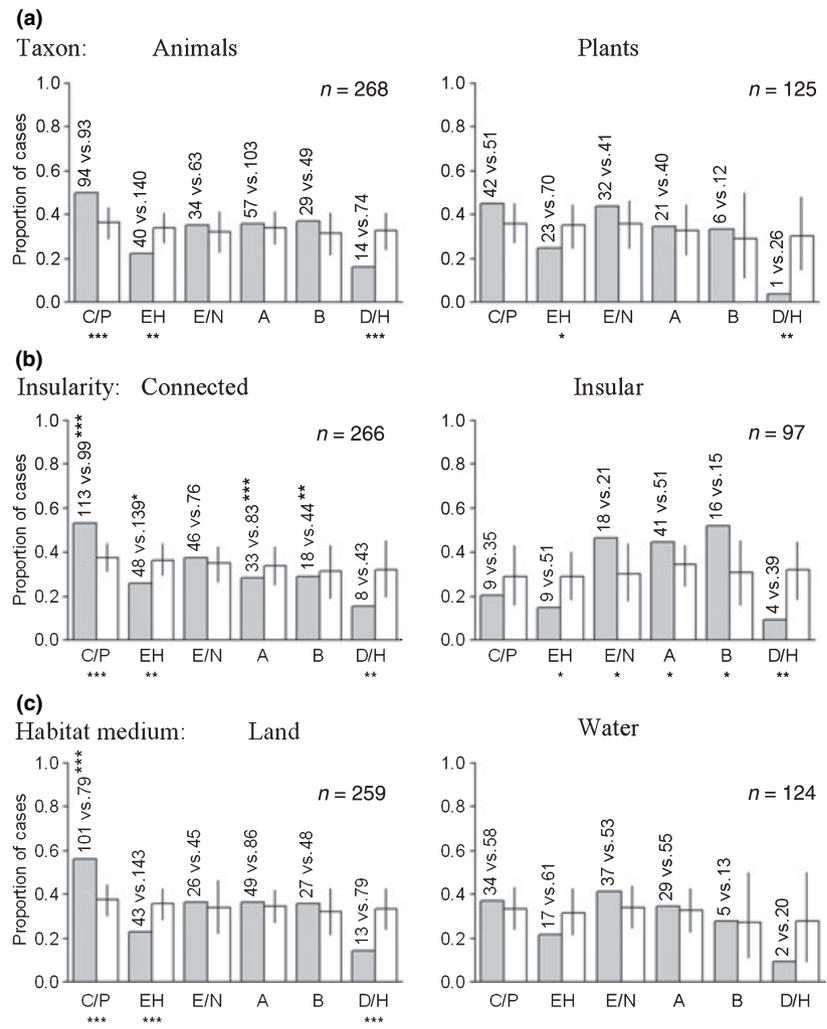


Figure 2 Primacy with respect to three grouping variables: (a) taxon, (b) insularity and (c) habitat medium. Presentation as in Fig. 1, except for the asterisks above the shaded bars: these compare the primacy of each correlate type across each grouping variable (e.g. area's primacy for plants compared with that for animals), using the same significance bands. The n in the top-right corner of each graph represents the total number of cases in the category (e.g. 97 data sets were exclusively insular systems).

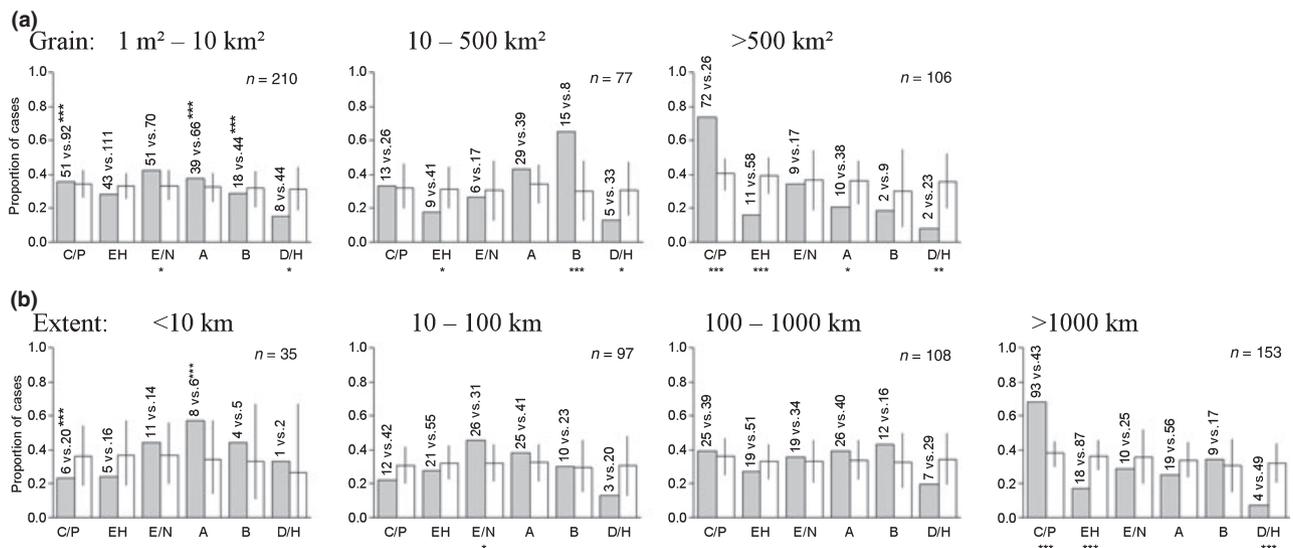


Figure 3 Primacy with respect to scale-related grouping variables: (a) grain size and (b) geographic extent. Presentation as in Fig. 2.

productivity had much higher primacy in terrestrial than in aquatic/marine species data sets (Fig. 2c). No other correlate type differed significantly in primacy between land and water.

In water, none of the primacies differed significantly from the null expectation; the overall pattern (Fig. 1) is driven by land environments. There were profound differences in primacy

Extent (km)	Grain (km ²)			Total	Extent (km)	Grain (km ²)			Total
	< 10	10–500	> 500			< 10	10–500	> 500	
Plants				Animals					
< 10	16			16	< 10	19			19
10–100	38	2		40	10–100	52	5		57
100–1000	27	10	2	39	100–1000	31	30	8	69
> 1000	8	8	14	30	> 1000	19	22	82	123
Total	89	20	16	125	Total	121	57	90	268
Insular				Connected					
< 10	2			2	< 10	33			33
10–100	24	4		28	10–100	61	2		63
100–1000	8	25	4	37	100–1000	48	15	5	68
> 1000	2	25	3	30	> 1000	17	1	84	102
Total	36	54	7	97	Total	159	18	89	266
Terrestrial				Non-terrestrial					
< 10	15			15	< 10	15			15
10–100	55	3		58	10–100	32	4		36
100–1000	43	28	8	79	100–1000	15	12	2	29
> 1000	21	21	65	107	> 1000	4	9	31	44
Total	134	52	73	259	Total	66	25	33	124

Table 4 Number of cases in our data set (i.e. data sets meeting our criteria – see Materials and Methods), tabulated across each non-scale grouping variable, within each scale class.

between smaller and larger grains and extents (Fig. 3). In particular, primacy of climate/productivity was much higher at the largest grain and extent. Primacy of area showed a weaker

Table 5 Details of the other correlate types tested when each type is primary. (a) The mean number of hypothesis types tested per analysis (including the primary variable). (b) The distribution of correlate types tested in the analyses: each row shows the number of times each correlate type was tested for when the one indicated in the first column was primary. The numbers in bold indicate how many times each correlate type was primary in our data set. See Table 1 for classification scheme.

Primary	Correlate types tested						SE
(a)							
C/P	2.68						0.07
EH	2.89						0.10
E/N	3.08						0.11
A	3.08						0.10
B	3.40						0.19
D/H	3.07						0.30
Primary	C/P	EH	E/N	A	B	D/H	
(b)							
C/P	136	92	45	49	20	22	
EH	39	63	21	34	9	16	
E/N	54	41	66	27	11	4	
A	25	50	22	78	18	47	
B	21	21	12	20	35	11	
D/H	5	6	4	13	3	15	

C/P, climate/productivity; EH, environmental heterogeneity; E/N, edaphics/nutrients; A, area; B, biotic interactions; D/H, dispersal/history.

trend in the opposite direction (probably because there are relatively few insular cases at the largest scales). Biotic interactions had high primacy at the intermediate grain (10–500 km²), although the sample size was quite small.

We now examine some of these effects in more detail. First, the greater primacy of area in insular than in connected systems seems exaggerated at the largest scales: at the largest extent and grain (in combination), area is primary in only two out of the 37 cases in which it was tested in non-insular systems, but in all three of the insular systems. Second, dispersal/history was primary only in 9% (four of 43) of the cases in which it was tested in insular systems. This is not significantly different from the equivalent figure of 16% (eight of 51) for non-insular systems (Fig. 2; χ^2 test: $P = 0.35$). Finally, the notion that climate should dominate explanations for diversity gradients at large scales is supported, whether ‘scale’ is defined by grain or extent (Fig. 3, Table 6). Climate/productivity is the only one of the correlate types that increases in primacy both from smaller to larger grains and from small to large extents. The median grain size and extent of cases where a climate/productivity variable was primary ($n = 136$ cases, median grain size > 500 km², median extent > 1000 km) are larger than those in which a climate/productivity variable was tested but was not primary ($n = 144$ cases, median grain size < 10 km², median extent 100–1000 km; Mann–Whitney U -tests: $P < 0.001$ for both). Table 6 presents a scale framework that should be useful for work on diversity gradients. It illustrates the increase in the primacy of climate/productivity with increasing scale. The clearest picture is obtained for the large subset of studies that are both terrestrial and non-insular: primacy of climate in these cases was over 75% at the largest grains and extent (Table 6d).

Table 6 Scale framework, in which the extent classes are rows and the grain classes are columns. (a) The number of cases in the full data set at each scale. (b) Mean coefficient of determination (r^2_{adj}) for cases at each scale (± 1 standard error of the mean). (c) Primacy for climate/productivity variables, with the number of times primary/total number of times analysed in parentheses. (d) Primacy for climate/productivity variables in cases of non-insular, terrestrial habitats. Spearman's rank correlation between grain class and extent class for the whole data set: $\rho = 0.694$, $P < 0.001$; the top-right cells in the framework are empty by definition, which constitutes part of the correlation. Note the high primacy of climate/productivity at large scales (indicated by bold font).

Extent (km)	Grain (km ²)			Total
	< 10	10–500	> 500	
(a)				
< 10	35			35
10–100	90	7		97
100–1000	58	40	10	108
> 1000	27	30	96	153
Total	210	77	106	393
(b)				
< 10	0.46 \pm 0.041			0.46 \pm 0.041
10–100	0.44 \pm 0.025	0.64 \pm 0.072		0.46 \pm 0.025
100–1000	0.43 \pm 0.029	0.55 \pm 0.040	0.57 \pm 0.074	0.49 \pm 0.023
> 1000	0.51 \pm 0.049	0.64 \pm 0.035	0.59 \pm 0.021	0.59 \pm 0.017
Total	0.45 \pm 0.016	0.59 \pm 0.026	0.59 \pm 0.020	0.52 \pm 0.012
(c)				
< 10	0.23 (6/26)			0.23 (6/26)
10–100	0.22 (11/51)	0.33 (1/3)		0.22 (12/54)
100–1000	0.39 (17/44)	0.27 (4/15)	0.80 (4/5)	0.39 (25/64)
> 1000	0.77 (17/22)	0.38 (8/21)	0.73 (68/93)	0.68 (93/136)
Total	0.36 (51/143)	0.33 (13/39)	0.73 (72/98)	0.49 (136/280)
(d)				
< 10	0.08 (1/12)			0.08 (1/12)
10–100	0.21 (6/29)	1.00 (1/1)		0.23 (7/30)
100–1000	0.48 (16/33)	0.67 (4/6)	0.75 (3/4)	0.53 (23/43)
> 1000	1.00 (12/12)	1.00 (1/1)	0.76 (45/59)	0.81 (58/72)
Total	0.41 (35/86)	0.75 (6/8)	0.76 (48/63)	0.57 (89/157)

How well do primary variables correlate with species-richness gradients?

Across all cases, the primary variable accounts for $54.2 \pm 1.1\%$ (mean ± 1 SE, unadjusted r^2) of the variance in species richness. The equivalent figure for r^2_{adj} is $51.7 \pm 1.2\%$. The r^2_{adj} values are remarkably consistent across categories: whereas in the raw data they range between -0.06 and 0.98 , their means differ only slightly when categorized into correlate types, or according to the different grouping variables (Table 7). The r^2_{adj} values for edaphics/nutrients were significantly lower than those for area and climate/productivity, after Bonferroni correction. The differences between correlate types account for 10% of the variance in one-way ANOVA (Table 7) or 5% of the variation in the minimal adequate model (Type III sum of squares; Fig. 4b). In other words, no one correlate type is consistently much stronger than the others when it is the strongest correlate of species richness.

The r^2_{adj} of the primary variable could be affected by the number of explanatory variables tested together. Climate/productivity is tested against significantly fewer other correlate types on average than the other categories, which might be expected to reduce its average r^2_{adj} when primary (from a sampling effect: the highest r^2_{adj} is likely to be higher the more variables are tested). However, our data show that r^2_{adj} values for primary variables do not increase when more correlate

types are tested. In fact, there is a weak trend in the opposite direction: across all 393 cases there is a slight negative relationship (Spearman's rank $\rho = -0.19$, $P < 0.001$). Across the 257 cases for which climate/productivity is not primary, this negative correlation is slightly stronger ($\rho = -0.23$, $P < 0.001$), and it is non-existent for the 136 cases for which climate/productivity is primary ($\rho = -0.05$, $P = 0.57$).

Mean r^2_{adj} values tend to increase with grain size (Table 7, Fig. 4a), consistent with the notion that species richness in smaller plots correlates less well with single explanatory variables (for a discussion of this, see O'Brien, 2006). This is the strongest effect in the one-way ANOVAs for the grouping variables, but the model accounts for only 8% of the variation in r^2_{adj} values. O'Brien (2006) suggests that gradients over very large extents should have high average coefficients of determination (and be dominated by climatic variables). This is supported by the one-way ANOVA (Table 7) and by the scale framework (Table 6b). However, extent does not appear in the minimal adequate model, suggesting that its effect is not significant when other factors are accounted for. There is a strong correlation between extent and grain (Spearman's $\rho = 0.69$, $P < 0.001$), such that both account for much of the same variance in r^2_{adj} values, but grain is consistently the stronger correlate in our analyses.

The one-way ANOVAs for taxon, habitat medium and insularity account for 1–1.5% of the variation, with mean r^2_{adj} values ranging between 0.47 and 0.56 (Table 7). A slightly

Table 7 Results from one-way ANOVAs of adjusted coefficients of determination (r^2_{adj}) of primary explanatory variables with respect to the class of the primary explanatory variable, and the environmental and scale grouping variables. Also given are the mean r^2_{adj} (± 1 SE) for each category; the proportion of the variation accounted for by each ANOVA; and the primacy for the correlate types (no. of cases when primary/no. of cases when analysed but not primary). See Materials and Methods and Table 1 for classification scheme.

Factor	<i>n</i>	Probability	ANOVA r^2 [adjusted r^2]	Category	Mean r^2_{adj}	<i>n</i>	Primacy
Correlate type	393	< 0.001	0.104 [0.093]	Climate/productivity	0.558 \pm 0.019	136	0.49
				Env. heterogeneity	0.476 \pm 0.034	63	0.23
				Edaphics/nutrients	0.364 \pm 0.024	66	0.39
				Area	0.588 \pm 0.024	78	0.35
				Biotic interactions	0.528 \pm 0.039	35	0.36
				Dispersal/history	0.560 \pm 0.050	15	0.13
				Taxon	393	0.014	0.015 [0.013]
				Plants	0.473 \pm 0.021	125	
Insularity	363	0.049	0.011 [0.008]	Connected	0.501 \pm 0.015	266	
				Insular	0.557 \pm 0.024	97	
Habitat medium	383	0.021	0.014 [0.011]	Terrestrial	0.536 \pm 0.015	259	
				Non-terrestrial	0.476 \pm 0.020	124	
Grain	393	< 0.001	0.085 [0.080]	1 m ² –10 km ²	0.451 \pm 0.016	210	
				10–500 km ²	0.590 \pm 0.026	77	
				> 500 km ²	0.589 \pm 0.020	106	
Extent	393	< 0.001	0.058 [0.051]	< 10 km	0.461 \pm 0.041	35	
				10–100 km	0.458 \pm 0.025	97	
				100–1000 km	0.486 \pm 0.023	108	
				> 1000 km	0.586 \pm 0.017	153	

clearer picture emerges in the minimal adequate model (Fig. 4), which accounts for *c.* 22% of the variance in r^2_{adj} values. The strongest and most significant effect in this model is the interaction between insularity and habitat medium (Fig. 4c). Thus the effects of insularity and habitat medium depend on each other: in water, r^2_{adj} values are higher for connected than for insular systems; on land there is no significant difference. The corollary is that in connected systems r^2_{adj} is higher in water than on land (this is because of the marine environments and not the freshwater ones), whereas for insular systems it is higher on land. Taxon is absent from the minimal adequate model, suggesting that the small and weakly significant difference in mean r^2_{adj} between plants and animals shown by the one-way ANOVA (Table 7) may be artefactual, and that richness gradients of plants and animals are equally predictable.

DISCUSSION

Our meta-analysis has identified a number of patterns in analyses of species-richness gradients, some expected and some less so. Perhaps our most surprising result was that the correlates of plant and animal species richness are very similar in both type and strength, in spite of the profound biological differences between these two groups. On the other hand, our other results support widely held opinions, as discussed below. In particular, the claim that species richness shows strong correlations with climate at large grains and extents, but less so at smaller scales, receives strong support from our study.

Hypotheses and grouping variables

Across scales, media, taxa and systems, climate/productivity tends to be the strongest correlate of richness (highest primacy), and is the only correlate type with significantly higher primacy than the null expectation (Fig. 1). However, climate is the outcome of complex physical processes on Earth and is not in itself a complete explanation for diversity patterns. As our study shows, the spatial co-variation between species richness and climate is evident – even though the single variables considered here are insufficient, alone, to describe the complex nature of climate. A satisfactory explanation of species-richness patterns must include an explanation of why covariation should occur between climate and richness.

Climate/productivity has particularly high primacy at larger grains and extents (Fig. 3). These findings accord with those of Wright *et al.* (1993), who had far fewer studies available to analyse. Much of this scale effect may simply represent different degrees of climatic variation: climate varies over larger distances than most of the other variables, and so (1) studies small in extent will sample a relatively small climatic range, and (2) variation in other influences on species richness will tend to average out to a greater degree at larger grains than is the case for climate. Nevertheless, the likelihood that a factor is the strongest correlate of richness depends on its ecological importance as well as on the design of the study. Thus our findings are consistent with the view that climate is very important in determining richness, and they help to quantify the grains and extents at which the two are most strongly correlated. They also suggest that the influence of

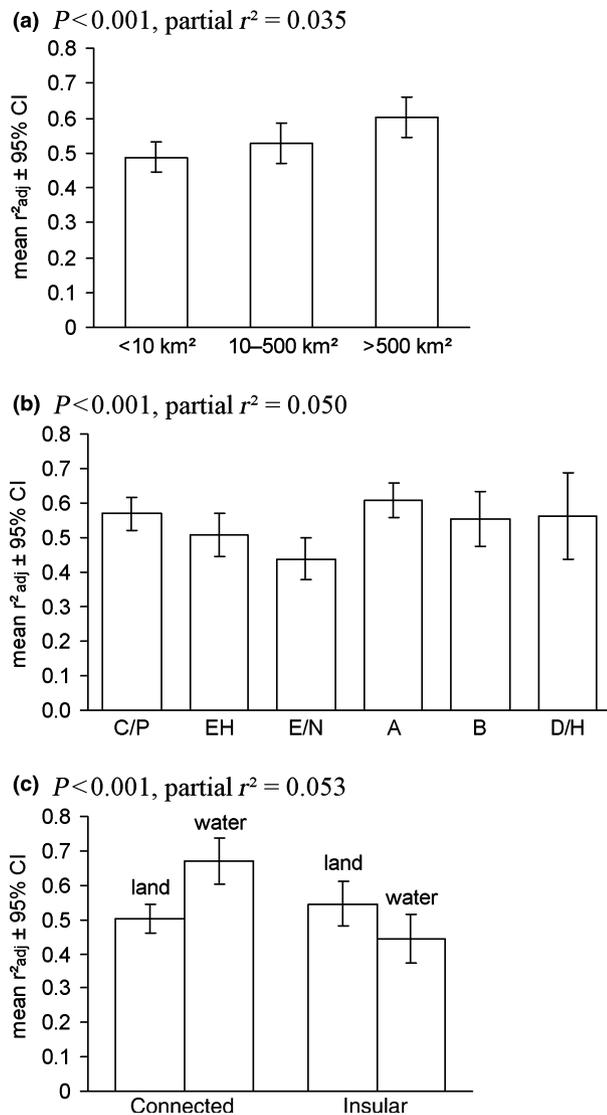


Figure 4 Estimated marginal means of r^2_{adj} for the effects in the minimal adequate model, which accounts for 21.8% (unadjusted; adjusted $R^2 = 0.195$) of the variance in r^2_{adj} values across cases. Estimated marginal means are the category means, once everything else in the model is accounted for (calculated using SPSS version 14); therefore they differ slightly from the equivalent means in Table 7. Panels (a) and (b) show the main effects of the significant factors not involved in an interaction: respectively grain and the correlate type represented by the primary correlate of richness. Type III P -values and partial r^2 s are shown. In (a) only the smallest and largest grains differ significantly. In (b) the only significant pairwise differences (after Bonferroni correction) are climate/productivity vs. edaphics/nutrients and area vs. edaphics/nutrients; see Table 1 for classification scheme. Panel (c) shows the interaction between insularity and habitat medium; this is the strongest effect in the model. All error bars represent 95% confidence intervals of the estimated marginal means.

climate is stronger in non-insular and terrestrial systems (Fig. 2). However, this effect may be artefactual. Studies of insular systems tend to be tropical more often than continental

studies, and thus the amount of variation in climate might be less. Furthermore, island studies are often restricted to a particular archipelago, in which climate varies little, whereas continental studies often include a wider range of climatic variation. In insular systems, we found area and biotic interactions to be more prominent in terms of primacy. However, continental studies are typically designed to minimize variation in area, whereas island studies are not – in fact, island studies often deliberately sample a wide range of island sizes. Thus the apparent influence of area for islands may be artefactual (more on this below), and the apparent reduction in the primacy of climate for insular systems may correspondingly be partly artefactual. A recent study by Kalmar & Currie (2007) is unique, to our knowledge, in that it directly compares continental and island richness. This study concluded that bird richness depends on climate and area in the same way in both systems.

The reduction in the primacy of climate in water compared with that on land (Fig. 2) is not surprising. A key innovation needed for terrestrial life is the prevention of water loss: water lost during respiration is very costly on land but not in water, especially freshwater, which represents the bulk of the non-terrestrial environments represented in our data. Climatic extremes tend to be ameliorated in water, and there is much less variability in the physical state of water (solid vs. liquid vs. gas) than on land. However, the lack of any significant increase in the primacy of any other correlate type in water is puzzling. Freshwater habitats tend to be closed, making biotic interactions potentially much more important there than in other habitats; trophic cascade effects are thought to be stronger in water-based communities than in land-based ones (Strong, 1992). Thus, it is surprising that we found no evidence of a greater importance of biotic interactions in non-terrestrial habitats, even given the relatively small sample size for this category. Moreover, all freshwater and marine ecologists are aware of the importance of water quality to plant and animal diversity. However, we found no significant difference in the primacy or r^2_{adj} of edaphics/nutrients between media, despite the reasonable sample size. Most terrestrial environments are essentially two-dimensional or narrowly three-dimensional, whereas lake and marine environments (particularly) are very much three-dimensional, with upward movement much less constrained by gravity in water. This leads to very different mixing and mobility: for instance, plants tend to be (passively) mobile as individuals in pelagic marine environments and in lakes, but not on land. However, we found no difference in the primacy or mean r^2_{adj} of environmental heterogeneity variables between terrestrial and non-terrestrial habitats.

The interaction between insularity and habitat medium in accounting for r^2_{adj} values (Fig. 4c) could be interpreted somewhat simplistically as follows: more variation in species richness tends to be accounted for on true islands (land) than in lakes and catchments (water), but for non-insular systems more variation is accounted for in oceans (water) than across continents (land). Why this should be is not clear, but it could be related to the age of the habitats: islands tend to be older

than lakes, for instance. It could also be related to the relative dispersal capabilities of the organisms across the study area. For example, terrestrial plants and animals might tend to disperse better across water than marine or aquatic plants and animals do across land. As with the age of the habitat, this could affect how close the system is to equilibrium with the hypothesized drivers of diversity, with richness variation in equilibrium systems being easier to account for than that in non-equilibrium systems. Further work is needed to test these possibilities.

Wright *et al.* (1993) found a large difference in median coefficients of determination between studies of animals (0.69) and plants (0.30). The needs of animals and plants differ in several important ways. In terms of consumable resources, both need water; however, sunlight is directly important for plants but not for most animals (other than solar ectotherms), whereas the tissue of other organisms is directly important for animals but not for most plants. More generally, plant food is primarily abiotic whereas animal food is biotic. Plants are typically also strongly influenced by soil, which responds to climate, whereas animals, terricolous groups notwithstanding, tend not to be. Animals are usually mobile throughout their lives, whereas plants are often only mobile as propagules; mobility should allow animals to avoid (macro)climatic extremes on short time-scales (e.g. diurnal). It is therefore surprising that we found no clear effect of taxon on either primacy or strength of correlation with richness patterns (our data: animal median $r^2_{\text{adj}} = 0.55$, plant median = 0.47; see also Table 7). The extent to which the differences between plants and animals affect the controls on spatial diversity patterns might be expected to depend on the spatial and temporal scales being considered, but comparing the plant and animal results using the spatial-scale framework illustrated in Table 6 shows remarkable consistency between plants and animals across scales, in terms of primacy of the various correlate types and the mean r^2_{adj} values (data not shown).

Wright *et al.* (1993) also found a very large difference, whereas we found only a small difference, in average coefficients of determination between climatic energy-related factors and other correlate types (their data: median $r^2 = 0.70$ vs. 0.23, respectively; our data: median $r^2_{\text{adj}} = 0.59$ vs. 0.50). In our analyses, there is not much difference between correlate types in mean r^2_{adj} values of the primary variables (Table 7, Fig. 4). However, two pairwise differences were significant: r^2_{adj} values tended to be lower when edaphics/nutrients variables were primary than when either climate/productivity or area variables were primary. Climate variables, therefore, were the most likely to be primary, and had relatively high r^2_{adj} values when primary.

Biotic interactions had the highest primacy at medium grain. The variation in biotic interactions at large grains, and to a lesser degree at large extents, could be under some climatic control (Whittaker *et al.*, 2003). We found only two cases in which biotic interactions are primary at the largest grain. In one of these (Andrews & O'Brien, 2000), the measure of 'biotic interactions', which was the best single-variable correlate of

mammal species richness in southern Africa, was the number of plant species/genera. When coupled with the direct and strong relationship between plant species richness and climate (O'Brien, 1993, 1998; O'Brien *et al.*, 1998), this finding was seen by the authors as emphasizing the indirect effect of climate on mammal richness patterns by means of plant-to-animal trophic exchange. Thus it was interpreted as both a biotic-interactions effect and a climate effect. In the other case (Danell *et al.*, 1996; Palaearctic data set), again of mammal richness, the measure of 'biotic interactions' that was primary was the percentage of the area that was forested. This variable, which was collinear with temperature and plot area, was one of the few cases in which we had difficulty in deciding the correlate type of the primary variable, and the extent to which percentage forest actually is a biotic effect is debatable. In short, we found limited evidence that biotic interactions are a primary explanation of richness patterns at grain sizes over 500 km². However, few studies examined biotic interactions at that scale ($n = 11$ cases), perhaps reflecting the difficulty of measuring them at the macro-scale, and of disassociating them from climatic control. Some macro-scale studies too recent for our data base have attempted this using structural equation modelling and found strong evidence for the role of biological interactions – for example Kissling *et al.* (2007, 2008), similarly to Andrews & O'Brien (2000), interpreted strong tree species-richness–bird species-richness paths as being indirect effects of climate on bird species richness. At smaller grains (< 10 km²), all measures of the diversity of other taxa, when primary ($n = 24$ cases), correlated positively with richness, supporting ideas of diversity begetting diversity – although it is also possible that all the taxa respond independently to the same external factors.

Area is much more likely to be the primary correlate of richness in insular than in connected systems (Fig. 2) and at smaller scales (Fig. 3), the scale effect being driven by connected systems (data not shown). Area's r^2_{adj} when primary tends to be relatively high, quite consistently so. These results are probably influenced by the measures of area used. Although we excluded studies examining only the form of the species–area relationship, many studies of islands encompass a wide range of island sizes. Almost all of these have variable grain size, with island area measured as a correlate of species richness, rather than area being kept constant in sampling. In contrast, studies on continents in our data set almost always use constant-sized quadrats, or political areas adjusted to be as constant in area as possible. Therefore, variability of grain differs markedly between insular and continental studies. The area hypothesis concerns more than just species–area effects: it mainly concerns the wider context of the plot or grid cell being studied (Rosenzweig, 1995, 2003). For example, species requiring large ranges will be present in plots within a large area of suitable habitat, but not in equivalent-sized plots on small islands. Furthermore, greater diversification can occur in large biome areas than in smaller ones, thus generating larger regional pools of species (note the overlap with historical richness and species pool hypotheses).

Such effects are most likely to be limiting on islands, and will often be captured by measuring island area. Measures of island area thus confound the two area effects (Turner, 2004): the causal effect *sensu* Rosenzweig, and the simple artefact of larger sampling areas tending to contain more species. Simple species–area effects are not relevant to studies of diversity gradients (Whittaker *et al.*, 2001). Combining the two effects in one measure tends to inflate the primacy and r^2_{adj} of the area variable. Furthermore, there is debate about the appropriate measures to use for larger land masses (Turner, 2004; Turner & Hawkins, 2004). Few non-insular studies even attempt to measure the area effect *sensu* Rosenzweig (e.g. biome area); the studies by Turner *et al.* (1988) and Hawkins *et al.* (2003b) are exceptions. Thus the ‘area effects’ being tested tend to vary between insular and non-insular cases. For these reasons, we consider that the difference between islands and continents in the primacy of area is largely an artefact of the methods used in the literature, and so we conclude nothing about any real causal effects.

The primacy of edaphics/nutrients does not differ significantly from null expectation, nor does it differ across any of the grouping variables. However, it has the lowest average coefficient of determination when primary (Table 7), significantly lower than those of climate and area. Most surprising is its near-identical primacy (Fig. 2c) and average r^2_{adj} (Mann–Whitney *U*-test: $P = 0.72$) in terrestrial and marine/aquatic environments. Nutrients (natural or derived from pollutants) are often considered to be a primary control on productivity and total biomass in marine and freshwater environments (e.g. Stevenson & Pan, 1999; Smith, 2001; Lotze & Milewski, 2004), especially at smaller scales. Therefore, the decrease in primacy of climate/productivity in water-based environments ought to be accompanied by an increase in primacy of edaphics/nutrients, but this was not the case. Our result does not challenge the importance of nutrients in water-based habitats, but it does suggest that nutrient levels and soil type correlate with richness to a similar degree in the non-terrestrial and terrestrial realms, respectively. Another surprising result is that neither the primacy of edaphics/nutrients nor their mean r^2_{adj} when primary differed between animals and plants, whether tested separately for land and water-based environments or lumped together. One might expect edaphics/nutrients to affect plant richness more than animal richness because typically they have more direct effects on the lives of plants.

The correlation between environmental heterogeneity and richness has been extensively studied, but its overall primacy is low, at 23%. When it is primary, the correlation with habitat or topographic heterogeneity is usually positive, in line with the literature on heterogeneity effects. The correlation with abiotic disturbance variables, however, is much more mixed, with positive correlations in about half the cases and negative correlations in the other half, suggesting that the effect of abiotic disturbance on richness is very context-dependent (see also Mackey & Currie, 2001). The low primacy of environmental heterogeneity is maintained across the grouping variables, consistent with a secondary role for

environmental heterogeneity, mostly modifying patterns set by other factors.

Dispersal/history is rarely the strongest correlate of richness in our analysis. It has the lowest primacy of the six correlate types, at 13%, and this is very consistent across grain, extent and the other grouping variables. Its mean r^2_{adj} when primary is similar to the other correlate types, but this is subject to considerable error, given the small number of cases for which it is primary. Given the strong arguments in the literature about the likely importance of historical contingency for species richness (e.g. Latham & Ricklefs, 1993; McGlone, 1996; Wiens & Donoghue, 2004; Hawkins *et al.*, 2006; Mittelbach *et al.*, 2007), our results may be considered surprising. Dispersal/history factors may be more relevant to patterns of endemic richness than to patterns of richness in general (Whittaker *et al.*, 2001; Vetaas & Grytnes, 2002). However, the difficulty of measuring historical influences on richness may partly explain the low primacy – dispersal/history is the least-tested correlate type at small extents. It is also relatively little-tested in non-terrestrial environments and, interestingly, at large grain sizes and for plants. Moreover, most of the correlates in this type measure dispersal limitation rather than differences in evolutionary history; there is a need for more studies measuring the effects of evolutionary history on diversity patterns. Furthermore, historical effects do not tend to be tested in plurality like some variables, reducing the likelihood of their being primary by chance. Finally, there is likely to be collinearity between climate and history at the global scale (Ricklefs, 2004; Wiens & Donoghue, 2004); in particular, temperature is collinear with the age of biomes, because of the progressive cooling of the higher latitudes since the Eocene (Zachos *et al.*, 2001; Turner, 2004).

The nature of the data

When evaluating the results of our analyses, it is important to remember that some caveats apply. First, following Hawkins *et al.* (2003a), we included only non-experimental data. This was because of the needs to include multiple correlate types and to compare across scales (macro-scale experimental testing of multiple effects on species richness is rarely, if ever, possible or ethical). Thus the studies are correlative, and attempts to determine causality are limited to evaluation of plausible factors. Accordingly, the patterns of correlation that we have identified across scales, habitat media, taxa and insularity are emergent trends and mask a great deal of variety and exceptions. In order not to dilute the main trends with too many disclaimers we have not dwelt on the caveats at length, but are aware of them. For example, it is possible that many of the animal data sets for which climate/productivity was primary would produce strong plant richness–animal richness correlations if examined using methods similar to those used by Andrews & O’Brien (2000) and Kissling *et al.* (2007, 2008), so classifying the primary effect as either climate/productivity or biotic interactions is open to interpretation.

Explanatory variables more generally are not always easy to classify into correlate types, and in some cases the classification depends on the context of the original study. Similarly, some variables are easier to measure than others, which could affect both the r^2_{adj} values and the identities of the strongest correlates of richness. However, this effect is not consistent in direction: a less tightly defined proxy (e.g. for heterogeneity) can lead to reduced r^2_{adj} because it does not capture an effect very accurately, but it can also inflate r^2_{adj} values by incorporation of unintended effects. Furthermore, many measured effects depend on the actual proxy chosen. For example, although it is relatively easy to classify a variable as 'climate', the extent to which that variable actually measures the climate is much less obvious. There is great variety in the biodiversity literature, and therefore in our data set, in the way that 'climate' is measured.

Classifications of grouping variables (plant/animal, insular/connected, etc.) was relatively straightforward. We have not analysed the effects of as many grouping variables as we would have liked – for instance, we did not examine growth-form effects because of the great variation in growth-form differences between taxonomic groups (e.g. within plants vs. within animals) and the fact that often studies are performed across all organisms within a taxonomic group. Different growth forms could cause different factors to be influential in controlling diversity patterns, not least because of differences in body size (Whittaker, 2004).

Some combinations of variables are much more strongly represented in the literature than others (see Results – Structure of the species-richness data); the under-represented classes represent gaps in the literature and place some limits on the present analysis. Understudied classes include non-terrestrial ones, especially marine environments. Furthermore, surprisingly, our data include only 16 plant cases at the large grain size. The multitude of small-grain studies ($< 10 \text{ km}^2$), mostly carried out at intermediate extents, probably reflects the relative ease and speed of data collection at such scales. However, there are few suitable (i.e. non-experimental) studies of richness patterns at very local extents, particularly for island systems. We suggest that there is a role for more local-extent, non-experimental work in order to build a more complete multi-scale picture of diversity patterns and their correlates.

CONCLUSIONS

We found that climatic and productivity-related variables tend to be the strongest correlates of species richness at large grains and extents. Their 'explanatory' power also tends to be relatively high at these scales. These results are even stronger in non-insular, terrestrial habitats. At smaller grains and extents, results are less clear-cut, in accordance with O'Brien's (2006) expectations. Variables quantifying dispersal/history are rarely the best correlates of species richness at any scale or for any particular class of study. However, because history is difficult to incorporate without collinearity into regression models, its importance may be underestimated in our analysis

(cf. Ricklefs, 2004; Wiens & Donoghue, 2004). A priority for future research on historical effects on richness will be to develop and test hypotheses that make explicit, strong predictions that are not confounded with the predictions of other hypotheses. The relatively low primacy of explanatory variables other than climate at large scales supports the view that influences on species richness that vary at finer scales tend to average out at larger grain sizes, unless under the control of something varying more broadly (Whittaker *et al.*, 2001), and are therefore not measured. The spatial scale of the maximum range of variation for any one correlate of species richness needs to be carefully considered when trying to evaluate its relevance.

The process by which the correlates of species richness are selected for analysis is far from uniform. The same is true for the techniques used to analyse richness. The variables used in the literature range greatly in the degree to which they can be regarded as proxies for the hypotheses that we tested. Some hypotheses are hard to evaluate because it is difficult to measure their proposed effects, as with historical contingency. Individual measures of climate and productivity tend to be more straightforward, but there is considerable variation among authors in which variables are chosen, and some climate variables (in particular) used are known to be much weaker correlates of species richness at macro-scales than others are. These considerations could explain the small differences that we found in average coefficients of determination of the strongest correlate. If we are to advance further in understanding species-richness patterns, we should aim for studies that incorporate the testing of a wide range of hypotheses and that are careful in their choice of variables used to quantify the hypothesized effects.

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BIOSKETCHES

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