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# Cross-scale variation in species richness–environment associations

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## ABSTRACT

**Aim** The scale dependence of many ecological patterns and processes implies that general inference is reliant on obtaining scale-response curves over a large range of grains. Although environmental correlates of richness have been widely studied, comparisons among groups have usually been applied at single grains. Moreover, the relevance of environment–richness associations to fine-grain assemblages has remained surprisingly unclear. We present a first global cross-scale assessment of environment–richness associations for birds, mammals and amphibians from 2000 km down to *c.* 20 km.

**Location** World-wide.

**Methods** We performed an extensive survey of the literature for well-sampled terrestrial vertebrate inventories over clearly defined small extents. Coarser grain richness was estimated from the intersection of extent-of-occurrence range maps with concentric equal-distance circles around fine-grain assemblage location centroids. General linear and simultaneous autoregressive models were used to relate richness at the different grains to environmental correlates.

**Results** The ability of environmental variables to explain species richness decreases markedly toward finer grains and is lowest for fine-grained assemblages. A prominent transition in importance occurs between productivity and temperature at increased grains, which is consistent with the role of energy affecting regional, but not local, richness. Variation in fine-grained predictability across groups is associated with their purported grain of space use, i.e. highest for amphibians and narrow-ranged and small-bodied species.

**Main conclusions** We extend the global documentation of environment–richness associations to fine-grained assemblages. The relationship between fine-grained predictability of a group and its ecological characteristics lends empirical support to the idea that variation in species fine-grained space use may scale up to explain coarse-grained diversity patterns. Our study exposes a dramatic and taxonomically variable scale dependence of environment–richness associations and suggests that environmental correlates of richness may hold limited information at the level of communities.

**Keywords**

**Biodiversity, macroecology, metabolic theory of ecology, scale, species richness, terrestrial vertebrates.**

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## INTRODUCTION

Significant strides in macroecology have promoted our understanding of broad-scale geographic gradients in species diversity. Specifically, it has been shown that across diverse groups of terrestrial organisms and at continental to global extents, climatic variables are excellent predictors of species richness at grains of 100–500 km (Jetz & Rahbek, 2002; Hawkins *et al.*, 2003; Currie *et al.*, 2004). However, scale (i.e. the spatial grain or resolution of analysis units) is likely to influence our perception of



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environment–richness associations and there is probably no scale-invariant determinant of geographic patterns of species richness (Rahbek, 2005; Nogués-Bravo *et al.*, 2008). Although there has been growing appreciation of the need to document and conceptualize the grain-dependence of determinants of species richness (Rahbek & Graves, 2001; Van Rensburg *et al.*, 2002; Nogués-Bravo *et al.*, 2008; Field *et al.*, 2009), empirical assessments to date have been strongly limited in the range of grains. Most prominent is the scarcity of fine-grained assemblage compositional data, critical for obtaining a full scaling relationship. Moreover, informative comparisons among groups are reliant on obtaining extensive cross-grain richness–environment associations over similar extents. Such cross-group comparisons have been limited, preventing an integrated and global understanding of the scaling of richness–environment associations.

It is generally assumed that contemporary and past environment are major controls of coarse grain richness, while disturbance, stochastic processes and biotic interactions dampen the strength of environment–richness associations at smaller grains (Whittaker *et al.*, 2001; Ricklefs, 2004; Wiens & Donoghue, 2004). There is select evidence for an increase in strength of the environment–richness association toward coarser grains (Wright *et al.*, 1993; Rahbek & Graves, 2001; Van Rensburg *et al.*, 2002; Currie, 2007). However, as sample size is usually decreased in tandem with increased grain size, statistical interpretation is somewhat compromised. In addition, the paucity of fine-grained assemblage compositional data has so far limited these analyses to coarse grains that are far beyond the size of conceivable biological communities. Documenting the degree to which species–environment associations are pertinent to smaller grains is of major relevance for delineating the range of applicability of climatic niche models, global change predictions and macroecological processes (Araújo *et al.*, 2005; Guisan *et al.*, 2007; Willis & Bhagwat, 2009).

Different species might experience and utilize habitats at different grains, which are limited by their perceptive ability and their lifetime home range (Kotliar & Wiens, 1990). Thus, species with smaller home ranges are likely to respond to environmental signals originating from a smaller range of grains, leading to finer-grained associations with the environment (Ritchie, 2009). Moreover, as both body size (Gaston & Blackburn, 1996) and, in certain instances, dispersal abilities (Lester *et al.*, 2007) are positively correlated with geographic range size, narrow-ranged species may display finer-grained environmental–richness associations than wide-ranged species. Amphibians are typically smaller and possess reduced geographic and home ranges compared with both mammals and birds (Hendriks *et al.*, 2009), and thus we predict the importance of abiotic predictors in amphibians to shift to finer grains. It has been shown that amphibians are more sensitive to environmental gradients than birds (Buckley & Jetz, 2008). However, such patterns can result from both fundamental differences in environment–richness associations, e.g. ecological contingencies such as amphibians' dependence on water, or scale shifts in which both clades display similar environmental associations, albeit at different grains. Separating these two alternatives requires a comparison of richness–environment associations between clades across a wide range of grains.

The scaling of environmental predictors, such as temperature, productivity and habitat heterogeneity, can identify the relevant spatial domains of influence of processes underlying richness patterns. For instance, temperature is postulated to alter speciation rates by affecting rates of molecular evolution, and is therefore expected, over evolutionary time, to affect species richness at the coarse scale of the regional species pool (Brown *et al.*, 2004). As the effect of temperature on richness, as formulated by the metabolic theory, is most direct for ectotherms we propose that this pattern will be most pronounced for amphibians.

It follows that any statements about potential determinants of geographic patterns of species richness require extensive cross-grain comparisons. Lack of world-wide high-resolution knowledge of species distributions precludes such an understanding at full geographic coverage, but trading coverage for resolution and using representative samples now make a global assessment possible. In this study we use distribution records for *c.* 18,500 species of birds, mammals and amphibians across 433 well-surveyed fine-scale assemblages and their surroundings to assess the global cross-scale behaviour of environmental predictors of species richness. Specifically, we ask the following questions: (1) how does the total predictive power of environment–richness associations change across grains, (2) how does the relative importance of specific environmental correlates vary across grains, and (3) to what degree do different vertebrate clades show similar scaling relationships? We expect that the emerging cross-scale patterns of environment–richness associations will facilitate synthesis and advance the appreciation of scale for integrating ecological and evolutionary explanations of geographic diversity gradients.

## MATERIALS AND METHODS

### Species lists

We conducted an extensive survey of the literature for well-sampled and thoroughly documented species inventories for terrestrial vertebrates over clearly defined small extents (and not including islands). After additional vetting with primary sources we included a large number of locations from Meese (2005) which contains documented, taxonomically standardized species inventories from terrestrial protected areas. We only included localities with inventories considered to be 'complete' by the original source. We identified the geographic boundaries of study locations using the World Database on Protected Areas 2009 Annual Release (http://www.wdpa.org) or digital gazetteers and manually checked and edited placement. Due to a lack of accurate georeferenced data in the Sahara, two additional assemblages were added at defined locations > 100 km from oases. In total, 433 assemblages contained at least one clade and 294 contained all clades (Fig. 1).

The determination of what spatial extent may represent an actual fine-grained assemblage is dependent on the preferred definition of this term (Ricklefs, 2008) and the grain in which its

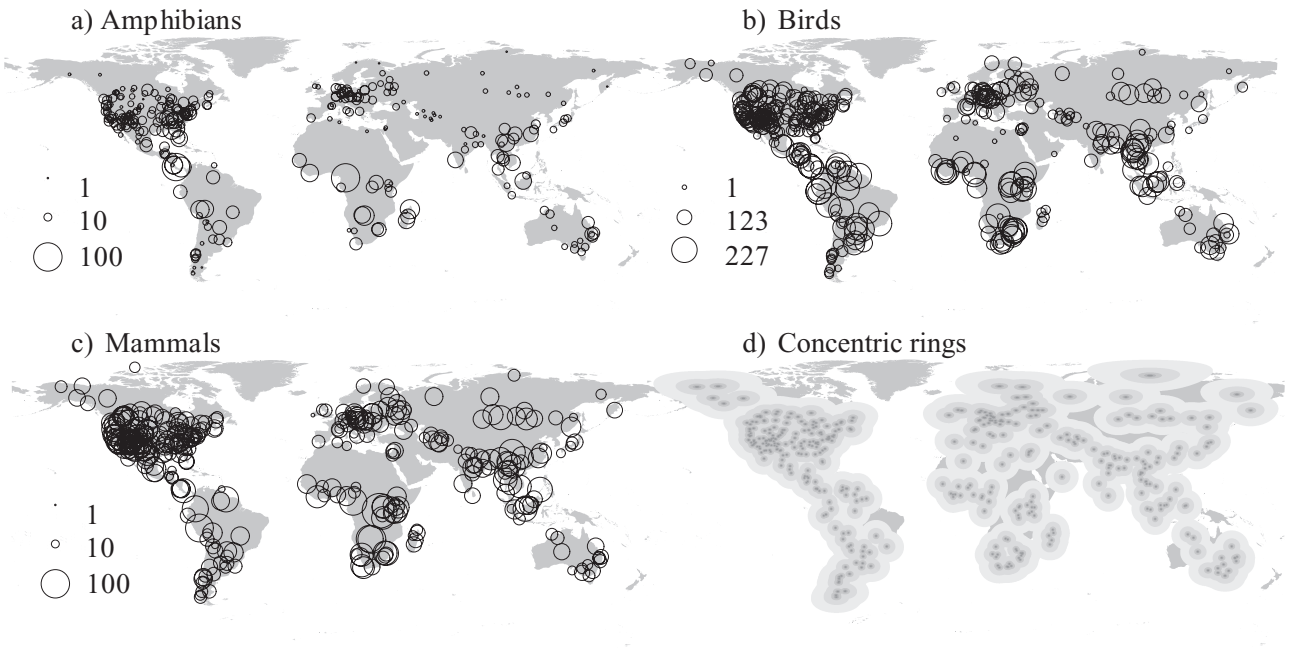


Figure 1 Fine-grained assemblage's richness patterns for the different clades (a–c) and the concentric rings around each assemblage used to estimate species richness at coarser grains (d). Circle diameters in (a)–(c) are proportional to species richness within fine-scale assemblages.

members interact with the landscape and each other. As a working definition for the purpose of this first global assessment, and given the obvious data limitation, we here consider assemblages censused from 10 to 7875 km$^2$ (median, 488 km$^2$; lower 25%, 108 km$^2$; top 75%, 1429 km$^2$) as fine-grained. Six additional assemblages from larger assemblages (8283–23,837 km$^2$) were added in noticeably underrepresented regions, including two in Amazonia, three in Siberia and one in West Africa. This range is an unavoidable caveat for a first overview at a global extent and acceptable regional coverage. For animals, no world-wide surveys exist that are standardized by area, and to our knowledge the data analysed here represent by far the most extensive compilation to date. Results remained qualitatively unchanged when the analysis was restricted to the middle 50% of assemblage areas (108–1429 km$^2$).

Coarse-grain richness was estimated based on the intersection of extent-of-occurrence range maps with concentric equal-distance circles around assemblage location centroids. These consisted of diameters of 100, 200, 500, 1000 and 2000 km (*c.* 0.8°, 1.6°, 2.3°, 8°, 16° near the equator). Nearby sites, especially at large grains, tended to overlap and were therefore not completely independent. Spatial non-independence is common in macroecological studies and was addressed by using spatial data analysis techniques (see below). We included all birds (breeding ranges only, 6059 species at fine-grain, 8924 at 2000 km diameter grain), terrestrial non-volant mammals (1846, 4922), and amphibians (1167, 4801), resulting in a total of 9192 fine-grained species and 18,647 species at 2000 km diameter grain. Range-maps were based on the IUCN assessment (http://www.iucnredlist.org/) for mammals (Schipper *et al.*, 2008) and amphibians (Buckley & Jetz, 2008). Distributions for birds were compiled from the best available sources for a given geographical region or taxonomic group (Jetz *et al.*, 2007).

We were careful to retain for analyses only well-surveyed local inventories. Migrants, vagrants and observational errors were excluded by limiting analysis to species found (based on range maps) within 100 km of the inventory location. To examine whether the relatively poor explanatory power found for mammalian fine-grained assemblages can be attributed to undersampling of small (often nocturnal) species, we performed a similar analysis after removing species with body masses < 100 g. This improved $R^2_{adj}$ values by only a small amount (from 0.08 to 0.16) and did not alter the general pattern. As expert range maps are prone to false presences when analysed at too fine a scale (Hurlbert & Jetz, 2007), we limited their use to 100 km diameters and coarser.

### Environmental predictors

We chose a subset of core environmental variables that are commonly used to examine environment–richness associations. Mean annual temperature (TEMP, °C × 10, between the years 1950–2000) was downloaded from the WorldClim database (http://www.worldclim.org/) at a resolution of 150 arcsec. While this resolution is misleading, as data are actually based on interpolation between sampling stations, the extent of our fine-grain assemblages should ensure sufficient accuracy. Annual net primary productivity (NPP; kg C × m$^{-2}$ × year$^{-1}$ × 0.0001) at 1 km resolution, averaged over the years 2000 to 2006, was obtained from the NASA Moderate Resolution Imaging Spec-

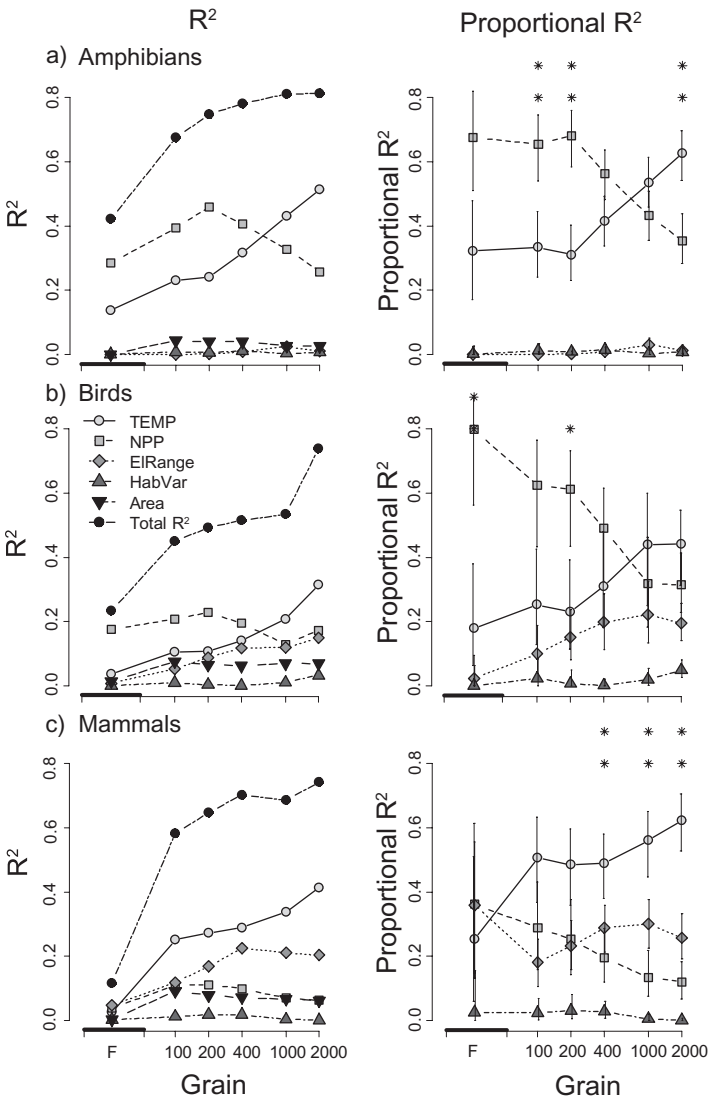


Figure 2 Grain-size dependence of species richness correlates. $R^2$ represents the hierarchical partitioning of total variance to the relative contribution of each of the environmental predictors: the left column is $R^2$ and the right column is proportional $R^2$ ($R^2$ for each variable divided by total $R^2$ across all predictors; the variable 'Area' was visually excluded). Error bars represent bootstrapped 95% confidence intervals. *F* represents the diameter (km, assuming circularity) of the fine-grained assemblages (interquartile range shown as a dark bar), while other values are the diameter around the fine-grained assemblage centroid. The asterisks denote models in which a significant ($P < 0.05$) difference between annual net primary productivity (NPP) and mean annual temperature (TEMP) was detected. Predictors include NPP and NPP$^2$, TEMP and TEMP$^2$, habitat variety (HabVar), elevation range (ElRange) and area (Area). Only sites containing all three clades were included.

troradiometer (MODIS) and calculated using the MOD17 algorithm. As annual precipitation correlated strongly with our measure of NPP ($r > 0.8$) we excluded it from analyses. Replacing MODIS-based NPP with alternative NPP measures or annual precipitation gave qualitatively similar results.

As measures of habitat heterogeneity we used the number of distinct land-cover types (HabVar) and the elevation range (ElRange, max – min elevation in metres). Land-cover types were extracted from the USGS Global Land Cover Characteristics (GLCC) database (http://edc2.usgs.gov/glcc/) with 96 vegetation classes and at 1 km resolution. A 30 arcsec elevation model (GTOPO30, US Geological Survey 1996) was used to calculate elevation range. All environmental predictors were $\log_{10} + x$-transformed prior to analysis [where $x = 1$ for most variables; for TEMP this value varied by scale (136–148) and was set so that the minimal value before log transformation was 1]. For some analyses TEMP was rescaled as $1/kT$, where $k$ is Boltzmann's constant (0.0000862), $T$ is the temperature in kelvin, and species richness was natural-log-transformed (Brown *et al.*, 2004; Hawkins *et al.*, 2007).

Total area varied both for fine-grained assemblages (due to their varying sizes) and at coarser grains (variable amount of land included). Therefore, at all scales, Area ($\log_{10}$ area in km$^2$) was included as a covariate in analyses. While this is a common procedure (e.g. Rahbek & Graves, 2001), it implicitly assumes the species–area relationships do not vary along geographical and environmental gradients. Although recent evidence suggests that this may be an unrealistic assumption (Storch *et al.*, 2005), for most grains we did not find a significant interaction between Area and other environmental variables (mammals, which displayed an interaction with NPP or TEMP at most coarse grains, but not for the fine-grained assemblages, were the exception). We also found low correlation between fine-grained Area and NPP ($r = -0.12$), negating the possibility that analyses were confound by large localities being restricted to low-productivity regions. Moreover, we found Area to be a generally poor predictor of richness, especially for fine-grained assemblages (Fig. 2) and repeating the analysis excluding Area did not alter our conclusions (Fig. S1 in Supporting Information). We therefore opted to consistently exclude an interaction between Area and

other variables to allow straightforward comparisons across grains and clades.

### Data subsetting

Sites captured a reasonable amount of global climate space but were not distributed evenly and tended to undersample extreme environmental combinations (Fig. S2). To minimize potential bias due to uneven sampling, we subset the data by randomly selecting a maximum of two points within a 5° cell (*c.* 550 km near the equator), thus leaving 305, 289 and 241 sites for birds, mammals and amphibians, respectively. To examine whether observed patterns are sensitive to range and body size variation we repeated analyses for the 40% most wide- and narrow-ranged and the 40% heaviest and lightest. Body mass was based on Dunning (2007) and Jones *et al.* (2009) and was supplemented with additional data. Genus averages were used for missing species. Lack of amphibian body mass data limited comparisons to birds and mammals. Sites with no species were excluded from the analyses. Qualitatively similar results were obtained when using different groupings such as quartiles.

### Spatial autocorrelation

We used simultaneous autoregressive (SAR) models to account for spatial autocorrelation, which is expected to increase with coarsening grain. Spatial error models were used, which introduce the autoregressive process in the error term, with row standardization. We examined a range of possible neighbourhood sizes (200–3800 km) for each model, grain and clade and chose the model with the lowest Akaike information criterion (AIC) score. Moran's *I* global test was used to determine whether residual autocorrelation persisted. Analyses were performed in the software R (R Development Core Team, 2008) using the package 'spdep'.

### Relative importance of environmental correlates

As richness is undoubtedly affected by multiple predictors, it may be less critical to find the 'correct' set of predictors rather than to quantify their relative importance. This task is not straightforward when these predictors are collinear, and model selection criteria, such as the AIC, perform poorly (Murray & Conner, 2009). We therefore used hierarchical partitioning to assess the average contribution of each predictor to the variance in species richness over all possible models (Grömping, 2006; Murray & Conner, 2009). We used the metric 'pmvd' in the R package 'relaimpo' which guarantees that predictors with an estimated coefficient of 0 are assigned a relative importance of zero.

To account for nonlinear associations of species richness and NPP or TEMP (even after appropriate transformation) the squared terms of these variables were added as additional predictors. Original predictors and their squared term were defined as a group and their relative importance was assessed as a single predictor. To account for spatial autocorrelation we first preformed a standard SAR model and then removed the spatial component of the fitted values. Richness excluding the spatial component was entered as a new response variable in the hierarchical partitioning procedure. The 95% confidence intervals for relative importance of the predictor and the difference between NPP and TEMP were obtained by bootstrapping model residuals (1000 iterations).

## RESULTS

Species richness exhibits distinctive geographical gradients across globally distributed nested subsets when moving from what we here consider fine-grained assemblages (median size 400 km$^2$) to coarser-grained assemblages of 100, 200, 500, 1000 and 2000 km diameter (Fig. 1). The ability of environmental variables to explain species richness decreases markedly toward finer grains and is lowest for fine-grained assemblages (Fig. 2). This decrease is robust to the concomitant changes in spatial autocorrelation (Fig. S3).

Comparing richness–environment associations over a large range of grains, we find that richness–environment associations varied strongly and consistently across grains in strength (relative importance; Figs 2 & S4) and shape (slope; Fig. 3, Table S1). Across taxa, environmental variables in amphibians retain importance to fine grains (*c.* 400 km$^2$) that is similar to that of birds and mammals at coarser grains (*c.* 8000 km$^2$; Fig. 2). In mammals and birds, fine-grained environment–richness associations are more important for narrow-ranged (the lower 40% of species) than for wide-ranged species (the upper 40%; Figs 4 & S5), even when controlling for spatial autocorrelation (Fig. S6). When comparing variation in environment–richness associations by body size (the lower and upper 40%, respectively), we find that small-bodied species tend to display elevated environment–richness associations, as predicted by the predominantly finer grain in which they perceive their environment (Figs 4, S7 & S8).

When comparing environmental predictors, we find a switch from high relative importance of productivity at fine grain sizes to high importance of temperature at coarser grains, observed for all clades and for both wide- and narrow-ranged species (Figs 2, S5 & S6). We find both temperature and productivity to have steeper slopes, and hence a stronger effect per unit increase, at coarser grains (Fig. 3). However, the partial slopes, removing the collinearity between these predictors, reveal a much steeper grain dependence for temperature (Fig. 5).

Analyses of relative importance demonstrate that climatic variables are consistently superior richness correlates than heterogeneity measures (Fig. 2). Habitat heterogeneity–richness associations are the steepest at grains of 100 to 400 km, while elevation range exhibits the steepest association with richness at coarse grains (Fig. 3). Consistent with other studies (Jetz & Rahbek, 2002; Ruggiero & Kitzberger, 2004; Rahbek *et al.*, 2007), narrow-ranged species displayed higher relative importance of elevation range than wide-ranged species (Figs S5 & S6).

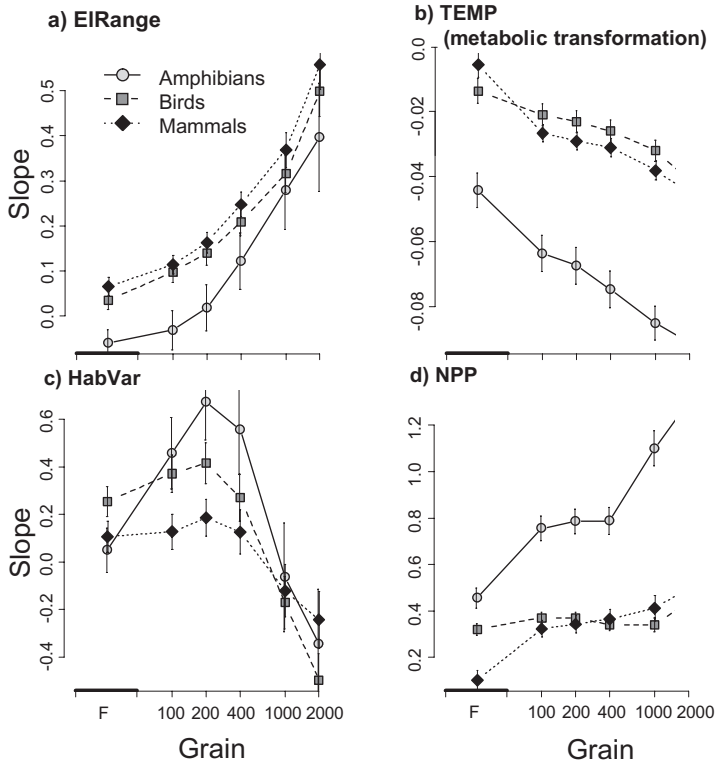


Figure 3 The slope of the single predictor linear regression between richness and environmental variables across grains. To facilitate comparison nonlinear relationships were not considered. All variables were $\log_{10}$-transformed apart from mean annual temperature (TEMP), which was recalculated to $1/kT$ where $k$ is Boltzmann's constant (0.0000862) and $T$ is the temperature in kelvin, and the corresponding richness which was natural-log transformed. Error bars represent $\pm$ 1 standard error. Presented results are the mean of 20 separate iterations. Predictors include annual net primary productivity (NPP), TEMP, habitat variety (HabVar) and elevation range (ElRange). One the *x*-axis (Grain), *F* represents the diameter (km, assuming circularity) of the fine-grained assemblages (interquartile range shown as a dark bar), while other values are the diameter around the fine-grained assemblage centroid.

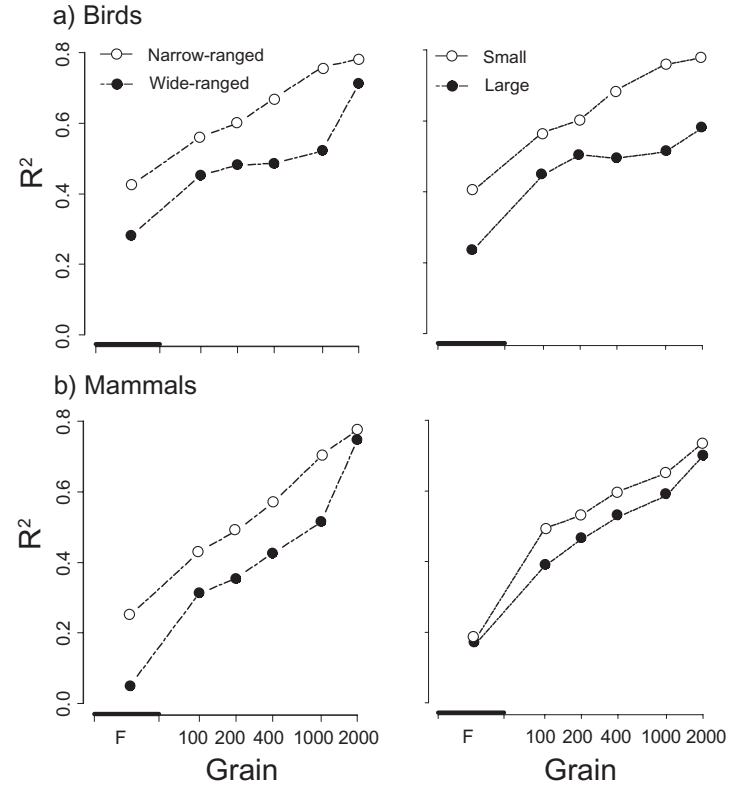


Figure 4 Deconstructing total $R^2$ of the environment–richness associations. Left column: narrow- (lower 40%) versus wide–ranged (upper 40%) species. Right column: small- (lightest 40%) versus large-bodied (heaviest 40%) species. All environmental variables were included. Limited sites with non-zero richness for narrow-ranged species and lack of body mass data prevented similar comparisons for amphibians. One the *x*-axis (Grain), *F* represents the diameter (km, assuming circularity) of the fine-grained assemblages (interquartile range shown as dark bar), while other values are the diameter around the fine-grained assemblage centroid.

## DISCUSSION

By comparing richness–environment associations over a large range of grains we demonstrate that variation across grains was frequently larger than variation across clades or environmental predictors. Consequently, patterns at single grains may be of limited ecological generality. The strong environment–richness associations found at coarse grains becomes markedly weak

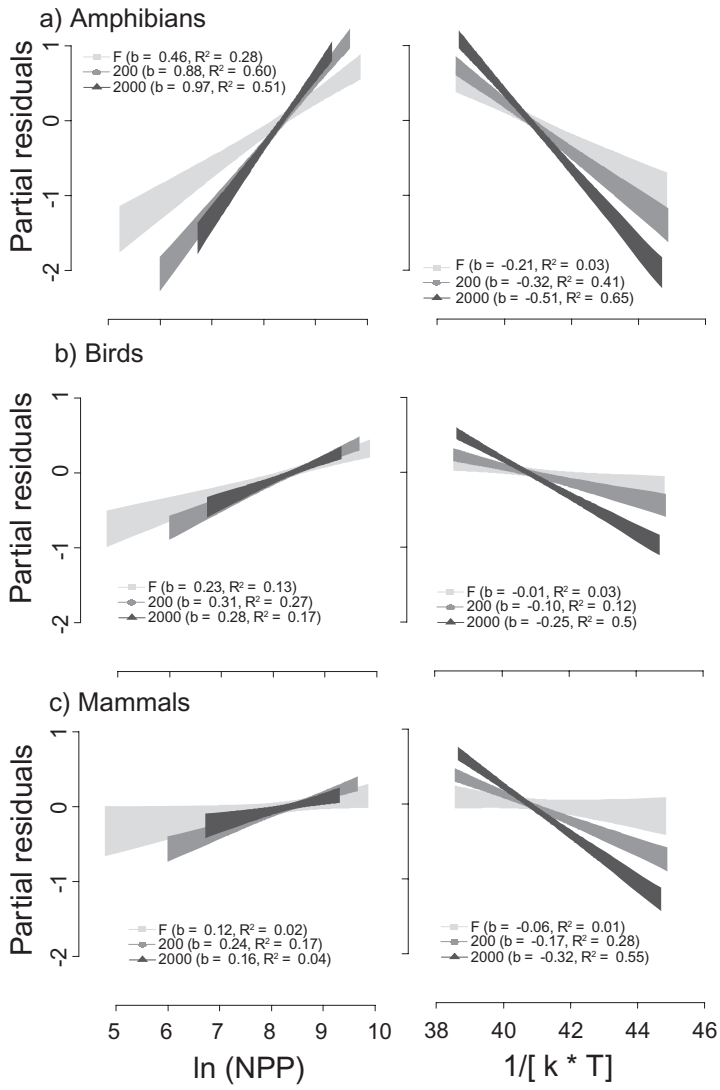


Figure 5 Partial residual plots. Right: mean annual temperature (TEMP) while controlling for annual net primary productivity (NPP) and NPP$^2$. Left: NPP while controlling for TEMP and TEMP$^2$. Within each graph three representative grains are plotted: fine-grained assemblage scale (*F*), 200 km and 2000 km diameter. Dark bands represent regression 95% confidence intervals. The partial regression coefficients (b) and the corresponding adjusted $R^2$ values are presented within each panel. To facilitate comparison with the literature, species richness and NPP were natural-log transformed while TEMP was rescaled as $1/kT$, where $k$ is Boltzmann's constant (0.0000862) and $T$ is the temperature in kelvins. Only sites containing all three clades were included.

toward finer grains. We note that the fine grain that has the weakest richness–environment associations (median of 400 km$^2$) could for terrestrial vertebrates reasonably be considered the grain at which species interactions take place, and at which conservation decisions are made. It follows that, despite the statistical strength and prominence of coarse-grain predictors of species richness, the processes underlying fine-grained richness gradients remain surprisingly poorly identified.

Although increased strength of environmental predictors from *c.* 100 × 100 km to coarser grains has been shown for birds in the Americas (Rahbek & Graves, 2001), the stark additional decrease of explanatory power toward grains below *c.* 10,000 km$^2$, and particularly its generality across the globe, have to date not been appreciated. All three clades displayed similar patterns, although sampling intensities at the finest grain are likely to differ greatly (highest for birds, lowest for mammals). Moreover, the inclusion of only well-sampled groups such as mammals > 100 g did not substantially improve model performance. Therefore, while variable sampling intensity may contribute to the variability in richness estimates at the finest grains, we do not believe this drives observed patterns. This suggests that while the environment may determine species richness at coarse grains, fine-grained richness may be predominantly regulated by other processes (Ricklefs & Schluter, 1993; Whittaker *et al.*, 2001; Ricklefs, 2004). Both biotic and abiotic filters may regulate the species from the regional pool that will appear in fine-grained assemblages through community assembly processes. As these filters act on species idiosyncratically, e.g. in relation to their traits and environmental adaptations, the overall result will be a weakening of the environment–richness association derived at broad scales. The ineffectiveness of our environmental models at fine grains highlights the importance of understanding better and, if possible, invoking local community assembly processes when modelling fine-grained patterns.

We predicted that the grains at which environmental conditions constrain species richness will differ across clades with different home ranges and dispersal abilities. We find that amphibians display elevated richness–environment association curves compared with birds and mammals, especially at small

grains. Thus, the richness–environment associations for three clades illustrate that the grain at which abiotic environmental factors gains prominence varies predictably with a clade's key ecological characteristics. Differences in geographic range size may reflect underlying dissimilarities in, for example, body mass and dispersal abilities, with narrow-ranged species being smaller and weaker dispersers than wide-ranged species (Lester *et al.*, 2007; Araújo *et al.*, 2008; Davies *et al.*, 2009). We find that fine-grained environment–richness associations in mammals and birds are more important for narrow-ranged than for wide-ranged species and for small-bodied than for large-bodied species. These results lend empirical support to the idea that variation in species fine-grained space-use may scale up to explain coarse-grained diversity patterns (Ritchie & Olff, 1999; Jetz *et al.*, 2004). Our findings offer only a first step in documenting these cross-scale connections, but as further data of broad extent and fine grain become available, we predict important advances in this area and an increasingly integrative, hierarchical understanding of species distributions that connects to individual-level ecological traits.

Environmental variables displayed strong and differential grain dependence (Figs 2 & 3), highlighting the limitation of comparing richness–environment associations based on single grains. As predicted, we find that temperature displays peak importance at coarse grains which is accompanied by a decrease in importance of productivity. This is consistent with the purported mechanism from metabolic theory, because temperature, via its effect on rates of evolution or biotic interactions, would most strongly affect richness at the level of the regional species pool. Metabolic theory also directly predicts the steeper temperature–richness associations found for the ectothermic amphibians. Alternatively, temperature could reflect current or historic coarse-scale limits to species distributions (Araújo *et al.*, 2008; Davies *et al.*, 2009; Pigot *et al.*, 2010). Increased steepness of latitude–richness associations with coarsening grain has been documented (Hillebrand, 2004), and as temperature strongly covaries with latitude, our results may provide a mechanistic basis for this pattern.

The near absence of grain dependence for productivity–richness associations, after accounting for collinearity with temperature (Fig. 5), suggests a mechanism which is either scale-invariant or predominantly operating at coarse grains. Productivity–richness associations differed among clades and were much steeper for amphibians, possibly reflecting their strong physiological limits (Buckley & Jetz, 2007). The more-individuals hypothesis predicts that larger populations in productive areas will reduce extinction rates with a differential response of rare and common species to energy availability (Evans *et al.*, 2005). As range size and local abundance are often correlated (Gaston *et al.*, 1997), this would translate to a stronger productivity–richness association for narrow-ranged species. However, we generally found wide-ranged species to have stronger associations with productivity (Figs S5 & S6), a pattern consistent with previous studies (Jetz & Rahbek, 2002; Ruggiero & Kitzberger, 2004; Rahbek *et al.*, 2007). Thus, the data may support other mechanisms, such as the niche position hypothesis, where energy influences rare resources that are exploited by specialist species, or the niche breadth hypothesis that postulates that higher energy increases the abundance of resources allowing for niche specialization.

There has been lingering controversy over the importance of heterogeneity measures, particularly elevation range, compared with climatic variables in explaining species richness (Kerr & Packer, 1997; O'Brien *et al.*, 2000; Ruggiero & Kitzberger, 2004; Davies *et al.*, 2007; Rahbek *et al.*, 2007; Ruggiero & Hawkins, 2008; Field *et al.*, 2009). Our analyses demonstrate that climatic variables are consistently superior richness correlates than heterogeneity measures. The superior predictive power of climatic variables may have been somewhat obscured in studies of regional extent where the range of climatic variability is greatly reduced. Some have emphasized a single mechanism supporting both elevation and climatic associations with richness (Ruggiero & Hawkins, 2008). However, in contrast to the case of climate, the slope of the elevation range–richness association was strikingly similar among clades (Fig. 3). This supports a distinct elevation–richness mechanism(s) common to all clades, such as barriers in mountainous regions, e.g. in interaction with oscillating past climates and resulting isolation dynamics, contributing to elevated allopatric speciation rates.

Our findings may also have broader implications for the use of climatic variables in environmental niche modelling (Guisan & Thuiller, 2005) and community modelling (Ferrier & Guisan, 2006) of species distributions. The decrease in strength of climatic predictors toward the fine grains typically used in environmental niche models (usually determined by the grain size of predictor variables rather than scale of putative mechanisms) does not inspire confidence that all critical aspects of climate–presence relationships are captured or best modelled at fine grains alone. Together with other evidence for strong grain dependence of species distributions predictors (Guisan *et al.*, 2007; Randin *et al.*, 2009), our findings point to hierarchical application of climatic variables in species distribution modelling (Pearson *et al.*, 2004). We acknowledge that, in our analysis, data limitations prevent inference about assemblages below 400 $km^2$, where we can expect biotic effects to be even stronger, and where the incorporation of categorical (non-climatic) fine-grain variables (e.g. vegetation and habitat type) may boost model performance (Randin *et al.*, 2009). However, even the best local environmental data may not be sufficient to fully explain fine-grained patterns and additional factors, such as regional environment or the size of the regional pool (White & Hurlbert, 2010), may need to be considered. Taken together, the strong scale effects documented here imply that general insights from single grain analyses about potential determinants of richness, comparisons among clades or predictors, and environmental models of community (and single-species) models of geographic distributions are limited. Instead, such efforts will benefit from documentation of entire richness-scale response curves and a careful matching between the grains of analysis and ecological inference.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1** Summary statistics for multiple-predictor models.

**Figure S1** Grain dependence of species richness correlates excluding the variable 'Area'.

**Figure S2** Principal components analysis (PCA) summarizing the range of environmental variability in grid cells with fine-grained assemblages.

**Figure S3** Grain dependence of species richness correlates after the spatial signal has been removed.

**Figure S4** Grain dependence of species richness correlates using single-predictor models.

**Figure S5** Grain dependence of species richness correlates for wide- and narrow-ranged species.

**Figure S6** Grain dependence of species richness correlates for wide- and narrow-ranged species after the spatial signal has been removed.

**Figure S7** Grain dependence of species richness correlates for large- and small-bodied species.

**Figure S8** Grain dependence of species richness correlates for large- and small-bodied species after the spatial signal has been removed.

## BIOSKETCHES

**Jonathan Belmaker** is interested in understanding how patterns of biodiversity and the underlying processes vary across scales and environmental gradients. He is particularly interested in the interplay between large-scale processes and local community assembly.

**Walter Jetz** is interested in the ecology, biogeography and conservation of terrestrial vertebrates and plants.

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