E-Article

More than "More Individuals": The Nonequivalence of Area and Energy in the Scaling of Species Richness

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abstract: One of the primary ecological hypotheses put forward to explain patterns of biodiversity is known as the more-individuals hypothesis of species-energy theory. This hypothesis suggests that the number of species increases along the global energy gradient primarily as a result of an increase in the total number of individuals that can be supported along that gradient. Implicit in this hypothesis is that species richness should scale with energy in the same way in which it scales with area in species-area relationships. We developed a novel framework for thinking about the interaction of area and energy, and we provide the first global test of this equivalence assumption using a data set on terrestrial breeding birds. We found that (1) species-energy slopes are typically greater than species-area slopes, (2) the magnitude of species-area and species-energy slopes varies strongly across the globe, and (3) the degree to which area and energy interact to determine species richness depends on the way mean values of species occupancy change along the energy gradient. Our results indicate that the increase in richness along global productivity gradients cannot be explained by more individuals alone, and we discuss other mechanisms by which increased productivity might facilitate species coexistence.

Keywords: species-area relationship, species-energy relationship, species richness, scale, birds, productivity.

Introduction

Understanding spatial variation in species richness has long been a central focus of ecology, but while we have gained a solid appreciation for empirical patterns, less headway has been made in evaluating underlying mechanisms. The difficulty is understandable given that geographical richness patterns are likely driven by a suite of ecological, evolutionary, and historical factors, many of which are statistically and biologically correlated. Recent directions in macroecological research have focused on exploring how potential mechanisms might unite species richness patterns with other canonical patterns in ecology (Harte et al. 2005; Storch et al. 2007, 2008; Arita et al. 2008; Gaston et al. 2008). This approach has been viewed as desirable both because of the appeal of creating a parsimonious theory linking multiple patterns and because such a theory provides for a greater number of tests (McGill 2003; McGill and Collins 2003). Often, identifying the ways in which such models fail can be even more instructive than identifying their successes.

One of the earliest such attempts to link two macroecological patterns was made by Wright (1983), who proposed a general model linking species-area relationships with positive productivity–species richness relationships. While a number of different mechanisms had been discussed for each, Wright (1983) identified one hypothesis that was common to both: that species richness is a positive function of the total number of individuals in an area. This idea came to be known in subsequent studies (e.g., Srivastava and Lawton 1998; Hurlbert 2004) as the more-individuals hypothesis. In quantitative form, this hypothesis can first be attributed to Preston (1962). He showed that species richness, S, should increase as a power function of the number of individuals N ($S \sim N^z$, where z is a constant) assuming that all assemblages exhibit lognormal abundance distributions. With the added assumption that the total number of individuals scales linearly with the product of per unit area resource availability $\overline{E}$ and area A ($N \sim \overline{E}A$), Preston (1962) presented a theoretical expectation for a species-area relationship power law. May (1975) showed that the power function relating species richness to number of individuals was a good characterization assuming any lognormal abundance distribution, and not only for the canonical form on which Preston focused. An implicit assumption of this derivation is that individuals are distributed randomly in space, which is rarely the case (Plotkin et al. 2000; Storch et al. 2007). Nevertheless, as a characterization of the form of the

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species-area relationship, the power law has been shown to be robust to variation in both abundance distribution and degree of intraspecific aggregation (Martin and Goldenfeld 2006).

While Preston (1962), May (1975), and a few others (e.g., Connor and McCoy 1979) noted that archipelagos with higher per-unit area densities of organisms should have species-area relationships with higher intercept values, area remained the fundamental variable of interest. By ignoring variation in $\overline{E}$ within an archipelago, these investigators effectively treated $\overline{E}$ as part of a constant that was distinct from the assumed variable of interest, area: $S \sim (\overline{E}^z)A^z$. Wright's (1983) primary contribution was to acknowledge that variation in $\overline{E}$ might be as important as variation in A for determining total abundance and, hence, richness, and his proposal essentially amounted to moving the set of parentheses: $S \sim (\overline{E}A)^z$. In so doing, he shifted attention to $\overline{E}A$—total resource availability—as the more general variable of interest, and he identified species-area relationships as the special case where $\overline{E}$ is constant. Analogously, he observed that the latitudinal diversity gradient across equal-area samples could be considered to be another special case in which $\overline{E}$ varied but area was held constant. Thus, Wright's (1983) species-energy theory provided an exciting general framework that could potentially unite two of the most common patterns in geographical ecology, and his compilation of data on the floras and avifaunas of 36 islands from across the globe generally supported this notion.

Over the past several decades, Wright (1983) has become a standard reference for those discussing available energy (used throughout this article as a synonym for resource availability) as a potential driver of richness patterns, and the vast majority of studies that have cited Wright (1983) up to now have indeed focused on the effects of $\overline{E}$ and have largely ignored A. By employing equal-area grid systems over all or part of the globe, investigators have been able to test for associations between richness and environmental variables controlling for the effects of area. Among such studies, available energy (estimated in the form of net primary productivity [NPP] or actual evapotranspiration) has garnered a great deal of support as a global predictor of species richness (e.g., Hawkins et al. 2003; Kreft and Jetz 2007; Whittaker et al. 2007), but so have a number of other variables with which it is often correlated (e.g., temperature, precipitation, habitat heterogeneity). Such are the inherent limitations of these sorts of correlational analyses. What only a handful of studies have appreciated is that Wright's (1983) framework linking area and energy allows for a more nuanced examination of both variables with the potential to yield deeper and more mechanistic insights. If area and energy both linearly affect the number of individuals that can be supported in an area, and if their sole effects on species richness occur via their effects on abundance, then the rate at which species richness increases with area will necessarily be identical to the rate at which it increases with energy. This will be true regardless of the particular mechanism linking higher abundances to higher richness, whether it is passive sampling of the regional species pool (Evans et al. 2005), reduced extinction rates (MacArthur and Wilson 1967), or some other process. However, if total abundance does not scale identically with area and energy, or if either area or energy has effects on richness that are independent of its effects via abundance, then the rates at which richness increases with area and energy will differ in a way that may suggest the importance of some diversity hypotheses over others. Here, we build on the framework put forward by Wright (1983) and explored by others (Wylie and Currie 1993; Storch et al. 2005, 2007) to conduct the first global test of the proposition that area and energy have equivalent effects in generating broadscale continental richness patterns.

Conceptual Models of Area and Energy Effects on Species Richness

We consider five models relating area A and average energy per unit area $\overline{E}$ to the species richness of broadscale assemblages, where each model is a subset of the general equation (see fig. 1)

$$\log S = c + z\log A + w\log \overline{E} + q\log A\log \overline{E}. \quad (1)$$

Models 1 (eq. [2]) and 2 (eq. [3]) are the cases in which each explanatory variable is considered independently of the other:

$$\log S = c + z\log A, \quad (2)$$

$$\log S = c + w\log \overline{E}. \quad (3)$$

These models are trivial in the sense that both variables are widely recognized to be important in explaining the richness of a region, and yet the models have both historical and comparative value. Historically, the vast majority of species-area relationships have been conducted while ignoring variation in energy availability within and among regions (Wright 1983; Rosenzweig 1995). Analogously, some researchers have tested for the effects of average energy, climate, or a surrogate (e.g., latitude) over regions varying substantially in area (e.g., Willig and Lyons 1998; Ricklefs et al. 2004); this practice is now less common with the use of equal-area grid-based analyses. The examination of these single-variable models is the basis for comparison of both parameter estimates and explan-

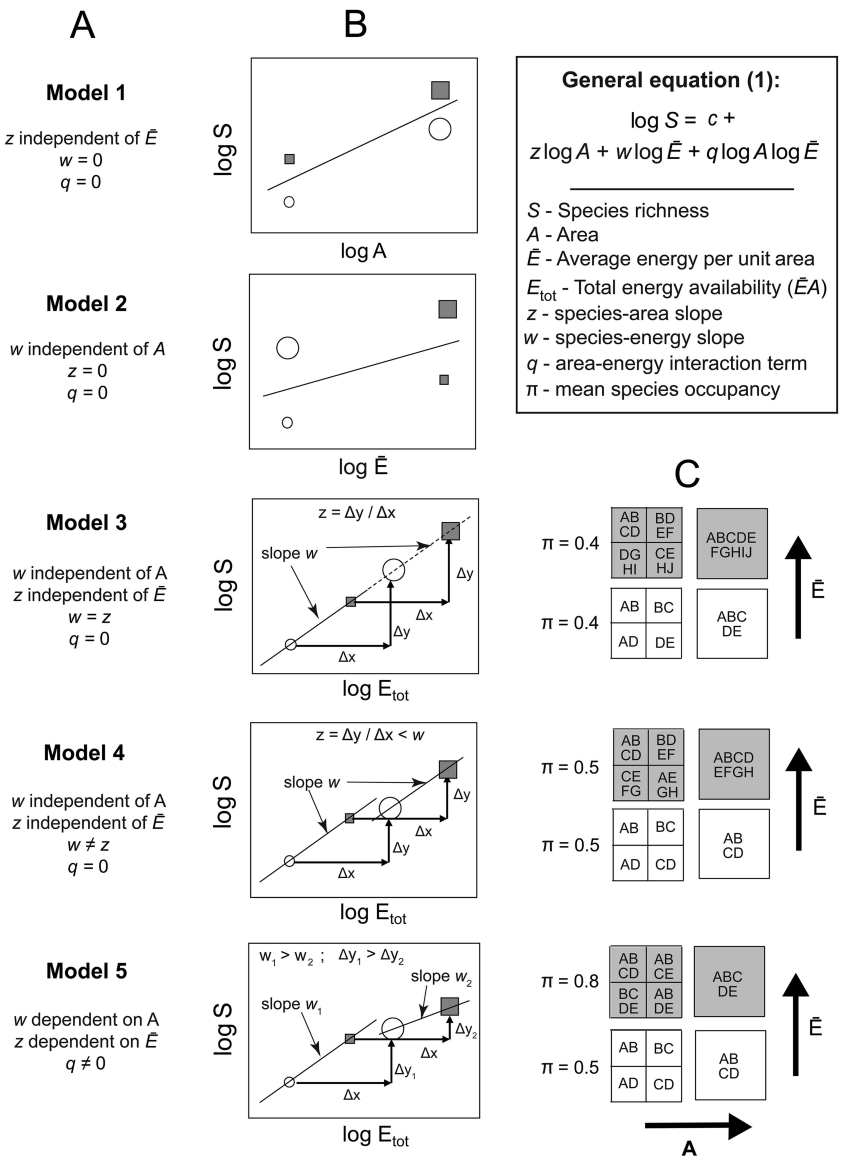

Figure 1: Conceptual overview of the five models representing equivalent or nonequivalent effects of area and energy that are examined in this study. Each model is a special case of the general species-area-energy model (eq. [1]). *A*, Constraints on the parameters *z*, *w*, and *q* for each model. *B*, Plots of richness as a function of area (*A*; model 1), average energy per unit area ($\bar{E}$; model 2), or total energy availability ($E_{tot} = \bar{E}A$; models 3–5) in log-log space for large and small regions (as indicated by symbol size) of low (*open*) and high (*shaded*) average energy availability. In models 1 and 2, only one of these variables is explicitly modeled, while the other is ignored. In models 3–5, the species-energy slope at a given spatial resolution, *w*, is the slope of the line between points of the same size but with different shading, while the species-area slope at a given energy level, *z*, is the slope of the line between points of the same shading but with different size, as determined from Δx and Δy. In model 3, the rates at which richness increases with area and with energy are identical, and thus, regardless of spatial resolution, there is a single characteristic species-energy relationship. In model 4, the slope of the species-area relationship ($z = \Delta y/\Delta x$) differs from that of the species-energy relationship *w*, and thus, the intercept of the species–total energy relationship varies with spatial resolution. Under model 5, the rate at which species richness increases with energy depends on area and vice versa. In this example, the slope of the species-area relationship is lower in a high-energy region ($\Delta y_2/\Delta x$) compared with a low-energy region ($\Delta y_1/\Delta x$), and the slope of the species-energy relationship is lower at a coarse resolution (w_2) compared with at a finer resolution (w_1). *C*, Hypothetical species distributions across nested quadrats and resulting mean occupancy values (π, the fraction of grid cells occupied by a species) for the regions depicted in (*B*). Because the species-area relationships treated here are based on nested quadrats, the species-area slope is directly linked to mean occupancy values. Letters represent unique species. In models 3 and 4, occupancy does not vary along the energy gradient, but the higher occupancy values of model 4 lead to shallower species-area slopes and hence an offset in intercepts when richness is plotted as a function of E_{tot}. If occupancy varies systematically along the energy gradient, then we expect to see a significant interaction term as in model 5. In this example, occupancy increases with energy, leading to shallower species-area slopes at high productivity. See text for more details.

atory power that allows inference about the joint effects of area and energy.

Model 3 is the model proposed by Wright (1983) that assumes that area and energy have equivalent effects on species richness, and it combines both effects into the single predictor total energy, $E_{\text{tot}} \equiv \overline{E}A$:

$$\log S = c + z\log E_{\text{tot}}, \tag{4}$$

$$\log S = c + z\log A + z\log \overline{E}. \tag{5}$$

In this model, a single slope is fitted to species-area and species-energy relationships when plotted in log-log space. The model implies that species–total energy relationships should lie along the same line regardless of spatial resolution. In the example shown (fig. 1), regardless of the mean energy availability of the region, a fourfold increase in area (Δx) leads to identical increases in species richness on a log scale (Δy).

Model 4 allows for the species-area and species-energy slopes to differ, and consequently, the intercepts of species-energy relationships plotted as a function of total energy availability will vary with spatial scale (fig. 1):

$$\log S = c + z\log A + w\log \overline{E}. \tag{6}$$

In the example shown, the rate at which species richness increases with area ($\Delta y/\Delta x$) is less than the species-energy slope within a given scale (w), although it could also theoretically be greater. The species distribution patterns on the right-hand side of figure 1 illustrate graphically what has been shown analytically, that species-area slopes are directly related to spatial patterns of turnover or beta diversity (Harte and Kinzig 1997; Koleff et al. 2003; Tjørve and Tjørve 2008) or, conversely, to mean species occupancies (Šizling and Storch 2004; Storch et al. 2005, 2007). In the model 4 example, species tend to occupy a greater fraction of quadrats within each region ($\pi = 0.5$) compared with the example depicted for model 3 ($\pi = 0.4$), and consequently, average beta diversity among quadrats is lower and species-area slopes are shallower. However, in both model 3 and model 4, average occupancy does not vary systematically with the mean energy availability of the region, and hence, species-area slopes ($\Delta y/\Delta x$) are independent of energy and species-energy slopes (w) are independent of area.

Model 5 allows for an interaction between area and energy such that species-area slopes vary with mean energy availability and species-energy slopes vary with spatial scale (eq. [1]). This implies that log S plotted as a function of log A and log $\overline{E}$ is a curved surface rather than a plane. Although such a function is inconsistent with Wright's (1983) power law–based framework, area and energy might still have equivalent effects on richness of a more complex nature (appendix in the online edition of the *American Naturalist*). An area-energy interaction is expected to be important if mean species occupancies vary systematically with energy availability. In the example depicted, mean occupancy and richness values of the low-energy region are identical to the low-energy region shown in model 4, but mean occupancy increases in the higher-energy region (fig. 1). As a consequence of the high occupancy values and, hence, a high compositional similarity among quadrats at high energy, a fourfold increase in area yields barely more species than the number found in a single quadrat. Thus, the species-area slope in the high-energy region is shallower than that in the low-energy region. If, as in this example, occupancy increases with energy availability, then the interaction term will be negative, but if occupancy were to decrease with energy availability, then the interaction term would be positive and species-area slopes would be greater at higher levels of energy availability.

Here we present the first global examination of nested species-area-energy relationships, using a data set of terrestrial breeding birds. First we assess across 107 equally sized regions of the world the relative support for models 1–5 on the basis of nested subsets of grid cells. We analyze and map out the regional variation in model support and parameter estimates, and we document the predictors of this variation and their potential causal underpinning. We pay specific attention to the role of occupancy, which is intricately linked to a mechanistic understanding of the potential interaction of energy and area.

Methods

Spatial Extent and Grains

We divided the globe into equal-area regions of 791,315 km^2 each (approximately 880 km or 8° on a side near the equator) and restricted analyses to the 107 regions with at least 80% land area (of these, 90 had at least 90% land area). Each region consisted of 64 grid cells of 110 × 110-km size (12,364 km^2 area, approximately 1° on a side near the equator) that were aggregated into nonoverlapping intermediate grains of 2 × 2 (16) or 4 × 4 (4) cells. The grid was compiled in an equal-area cylindrical projection. We deemed 110 km to be the finest grain size that, for the species distribution data set (see below), globally yields presence data with only negligible geographic variation in accuracy (Hurlbert and Jetz 2007).

Each region located entirely on land encompassed 85 data points, including all 64 1 × 1 cells, 16 2 × 2 cells, four 4 × 4 cells, and one value for the region as a whole. No data point with less than 80% land coverage at that

particular grain was included, and thus, some regions had fewer than 85 points.

Species Distribution and Environmental Data

We used extent of occurrence maps of the geographic breeding ranges of the world's 8,916 terrestrial bird species (i.e., excluding species that predominantly feed in aquatic habitats during the breeding season; for sources and details, see Jetz et al. 2007). We extracted species occurrences across each 110 × 110-km grid cell of the study's 107 focal regions. Because regions do not cover every part of the world, not all bird species were included in the final data matrix, which contained 6,043 species and a total of 1,270,092 grid cell occurrences. Species richness was calculated for each cell at each grain size as the total number of unique breeding distributions with at least one occurrence within the focal cell.

We used an estimate of annual aboveground NPP (g of carbon per m^2) from a recently developed global productivity model (Sitch et al. 2003). The model is based on the Lund Potsdam Jena dynamic global vegetation model and accounts for land use (Bondeau et al. 2007). We averaged model output across the years 1961–1990, summed monthly values to yield total annual NPP, and extracted the data (originally in 0.5° resolution) across the analysis grid cells. We replaced zero values in some areas that had extremely low productivity (e.g., the Sahara desert) with a value of 0.03, the lowest value recorded for this variable among all grid cells. For each cell and at each grain size, we calculated the mean (mean NPP) and sum (total NPP) of the NPP values for all constituent 1 × 1 cells. By definition, at the base resolution, mean NPP and total NPP were equal.

Assessment of Model Performance

Within each region, we fitted five different models to the $\log_{10}$-transformed species richness data (fig. 1). Because these models differ in complexity, we assessed model performance using the small sample–adjusted Akaike Information Criterion (AIC_c) and the AIC_c-derived Akaike weights (Burnham and Anderson 2002). Models with lower AIC_c values are considered to be better, and the Akaike weight can be interpreted as the relative support for a model among those considered.

We note that mean values of NPP at coarse grain sizes must be intermediate to the values of NPP at finer grain sizes within the region. This means that on a simple species-energy plot where area is variable, the data point representing the highest species richness (at the largest area) will occur midway along the *X*-axis. This will serve to elevate the estimate of the intercept of the species-energy relationship; however, these coarse-resolution data points will necessarily have very low leverage and thus are not expected to systematically bias the estimated slope.

Further caveats include the fact that regional analyses are conducted on nested subregions that are not independent and that the underlying species distributions exhibit spatial autocorrelation; these problems are common to all examinations of nested species-area relationships. We note that while these issues might pose problems for traditional significance testing, they are unlikely to influence parameter estimation (Hawkins et al. 2007), which is the focus of the study.

Predictors of Slope Variation

The rate at which species richness increases as a function of either area or NPP is of particular interest. We examined the degree to which variation in parameter estimates across the 107 regions could be explained by the following suite of regional variables: (1) mean NPP, (2) range in NPP, (3) elevational range, (4) habitat diversity, (5) the slope of the habitat-area relationship, and (6) mean weighted vertical habitat complexity. Regional mean and range of NPP were given by the grid cell–level data. Elevational range within a region was calculated using the GTOPO30 data set (USGS 1996), which has a resolution of 30 arc seconds. In order to assess major habitat types, we used a 30–arc second resolution global land cover map (USGS 2002) and counted the number of different land cover classes at different levels of aggregation (from one grid cell to the whole region). The classification we used is based on Olson (1994) and distinguishes 94 different ecosystem classes worldwide (ranging from one to 36 within a single 110-km grid cell). A region's habitat diversity was given by the number of unique land cover types. The habitat-area slope was calculated by plotting the number of land cover types present as a function of area for each cell of each grain size. Both axes were logarithmically transformed, and thus, this slope is directly analogous to a species-area slope and describes the rate at which new habitat types are encountered with increasing area.

Regional vertical habitat complexity was assessed as the mean value of vertical complexity of biomes present, weighted by their areal representation within the region. Indices of vertical habitat complexity were assigned by W. Jetz and ranged from 0 (least complex) to 7 (most complex); these can be found in the appendix. We used weighted linear regression to evaluate the importance of these variables on species-area and species-mean NPP slopes, weighting data points by the inverse of the standard error of the regional slope estimate. In so doing, slope estimates in which we have greater confidence are weighted more heavily in the model.

Finally, we calculated mean species occupancies at two scales: for each region as a whole and for each of the 16 nonoverlapping 2 × 2–grid cell subregions within each region. Mean occupancy ($\bar{\pi}$) was calculated as the mean across species of the fraction of cells occupied within a region or subregion. Occupancy at the regional level was correlated with species-area and species-energy slopes. In fact, Šizling and Storch (2004) showed that the expected analytical relationship between mean occupancy and the slope of the species-area relationship in log-log space is $z = -\log(\bar{\pi})/\log(A_{\text{tot}})$. We used our measure of mean regional occupancy to examine this relationship. Within each region, we also examined the strength of the relationship between mean occupancy within 2 × 2 subregions and mean NPP of those subregions. When this relationship is strong, we expect to find support for an interaction term in the species-area-energy relationship, and the sign of the correlation between these should be opposite the sign of their interaction.

Results

Variation in Model Performance

While spatial patterns of species richness and NPP were often correlated, the precise nature of the statistical relationship between them varied across regions (fig. 2). For some regions, richness increased at the same rate with both area and mean NPP (model 3) such that plots of richness versus total NPP for different spatial resolutions all lay along the same regression line (fig. 2*A*). In other regions, the rate at which richness increased with area and mean NPP differed, leading to offset intercepts (model 4; fig. 2*B*) and/or heterogeneous slopes (model 5; fig. 2*C*) in richness–total NPP plots across spatial resolution.

In comparing all 107 of the world's regions, we found that simple species-area relationships (model 1) rarely explained more than 50% of the variation in species richness within regions (fig. 3). While simple species-mean NPP relationships (model 2) occasionally explained a higher percentage, in more than 25% of regions they explained less than 10% of the variation (fig. 3). Wright's (1983) model assuming area-energy equivalency (model 3) has the same number of parameters as models 1 and 2, but it generally outperformed them. It explained more of the variation in intraregional species richness than did model 1 in 85% of regions (91 of 107), on average explaining 24.1% more of the variation. Likewise, model 3 explained more of the variation than did model 2 in 79% of regions (84 of 107), with an average gain in R^2 of 18.5%. Models 4 and 5 allow for the effects of area and NPP to vary independently, and by introducing more parameters it is not surprising that the average percentage of variation in richness explained increases above and beyond model 3. Model 5 explained more than 80% of the variation in species richness for more than 25% of the regions. In general, richness patterns were typically best explained in regions exhibiting clear geographic gradients in NPP, such as along the southern edge of the Sahara desert and at northern latitudes across Eurasia (figs. 2, 3; zip file).

While models 1–3 share the same number of parameters, models 4 and 5 are more complex, limiting the use of R^2 for evaluating model performance across the full set. Within each region, Akaike weights were calculated for the five models on the basis of ΔAIC_c values, and the distributions of weights across all regions are shown in the histograms of figure 3. None of the five models consistently and unambiguously outperformed all others, although models 1 and 2 consistently received virtually no support. Model 4 received the majority of support (Akaike weight >0.5) in 47 of the 107 regions, while model 5 and model 3 received the majority of support in 22 and 18 regions, respectively. In only a handful of regions did any model unambiguously outperform all of the other models, and these were all best fitted by model 5[1] (e.g., see fig. 2*C*).

Regions best fitted by model 5 occurred primarily across northern latitudes in Eurasia, as well as in the Himalayas and in a few scattered parts of South America, Africa, and North America (fig. 3). Model 3 received the most support in northern Africa and in parts of central and eastern Asia, southern South America, and Australia. Model 4 performed best across western North America, much of South America and central Africa, and scattered regions across Eurasia and Australia. Surprisingly, the simple species-area relationship (model 1) received the majority of support in four regions scattered across North America and sub-Saharan Africa. There were 16 regions in which no model had an Akaike weight greater than 0.5.

Variation in Slopes

Species richness generally increased at a faster rate with NPP than it did with area (fig. 4). This was the case for both univariate (models 1 and 2) and bivariate models (model 4). Note that, in model 5, area slopes vary as a function of NPP and NPP slopes vary as a function of area, so no meaningful comparisons can be made of those parameter estimates in that model. Spatial patterns of the

[1] It should be noted, however, that the structural difference between models 4 and 5 restricts the way in which the Akaike weights might differ. Because model 5 is simply model 4 plus one additional parameter (the interaction term), even if the additional parameter does not contribute at all to an increase in likelihood, the AIC for model 5 can never be more than 2 greater than the AIC for model 4. As such, model 4 can never have an Akaike weight greater than ~0.75. Conversely, the additional parameter might notably increase model likelihood, allowing much higher weights for model 5.

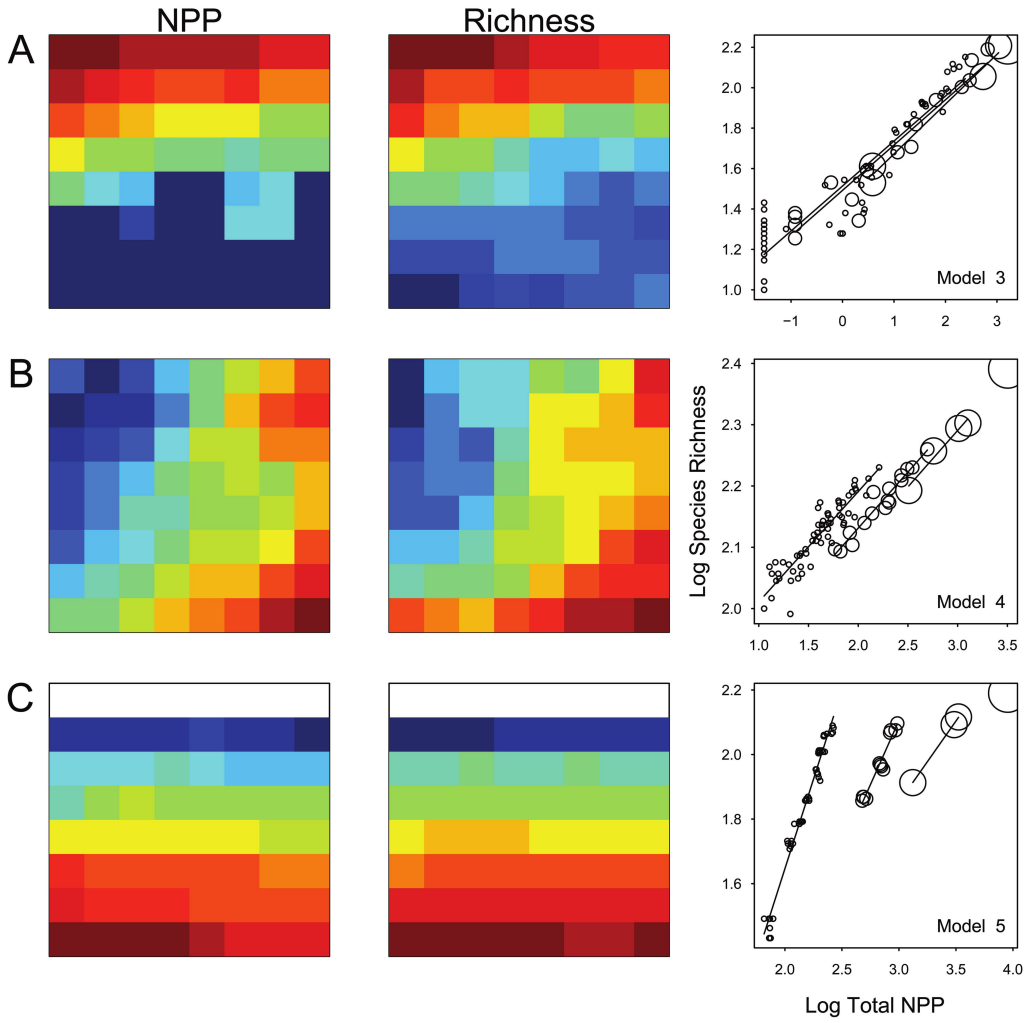

Figure 2: Richness-energy relationships for three example regions of 791,315 km^2. The first two columns depict the spatial variation in net primary productivity (NPP) and species richness, with higher values represented by warmer colors. The color scale is not comparable between maps. The third column shows how species richness increases as a function of total NPP at differing spatial resolutions, with coarser resolutions indicated by larger symbols (see "Methods"). The first region (*A*) is in north-central Algeria, encompassing the northern edge of the Sahara, and it is best fitted by model 3. The second region (*B*) is in the interior of northern New South Wales and southern Queensland in Australia, and it is best fitted by model 4. The third region (*C*) is in north-central Siberia and is best fitted by model 5. Exact locations are depicted in figure 3.

simultaneously estimated area and mean NPP slopes from model 4 are highly correlated with the slopes estimated in models 1 and 2 ($r = 0.962$ and $r = 0.997$, respectively), suggesting that area and mean NPP do not suffer from collinearity in this data set. On the basis of a mixed-effects model across regions (with region fitted as a random effect), the average species-area slope was 0.147 while the average species-mean NPP slope was 0.241. The nonnested nature of the species-mean NPP relationship and the greater variability in the range of mean NPP values (compared with the constant 64-fold variation in area within each region) each contribute to the greater variability observed in species-mean NPP slopes compared with species-area slopes. When the effects of area and mean NPP are combined into a single variable, total NPP, the range and spatial variation of parameter estimates are similar to those of the species-area model ($r = 0.75$). Estimates of the interaction term in model 5 ranged fairly symmetrically about 0; however, for those regions with a reasonable amount of support for model 5 over other models (i.e., for regions with a model 5 Akaike weight >0.5), this parameter tended to be negative, with a median value of -0.123.

The slope of both species-area and species-energy re-

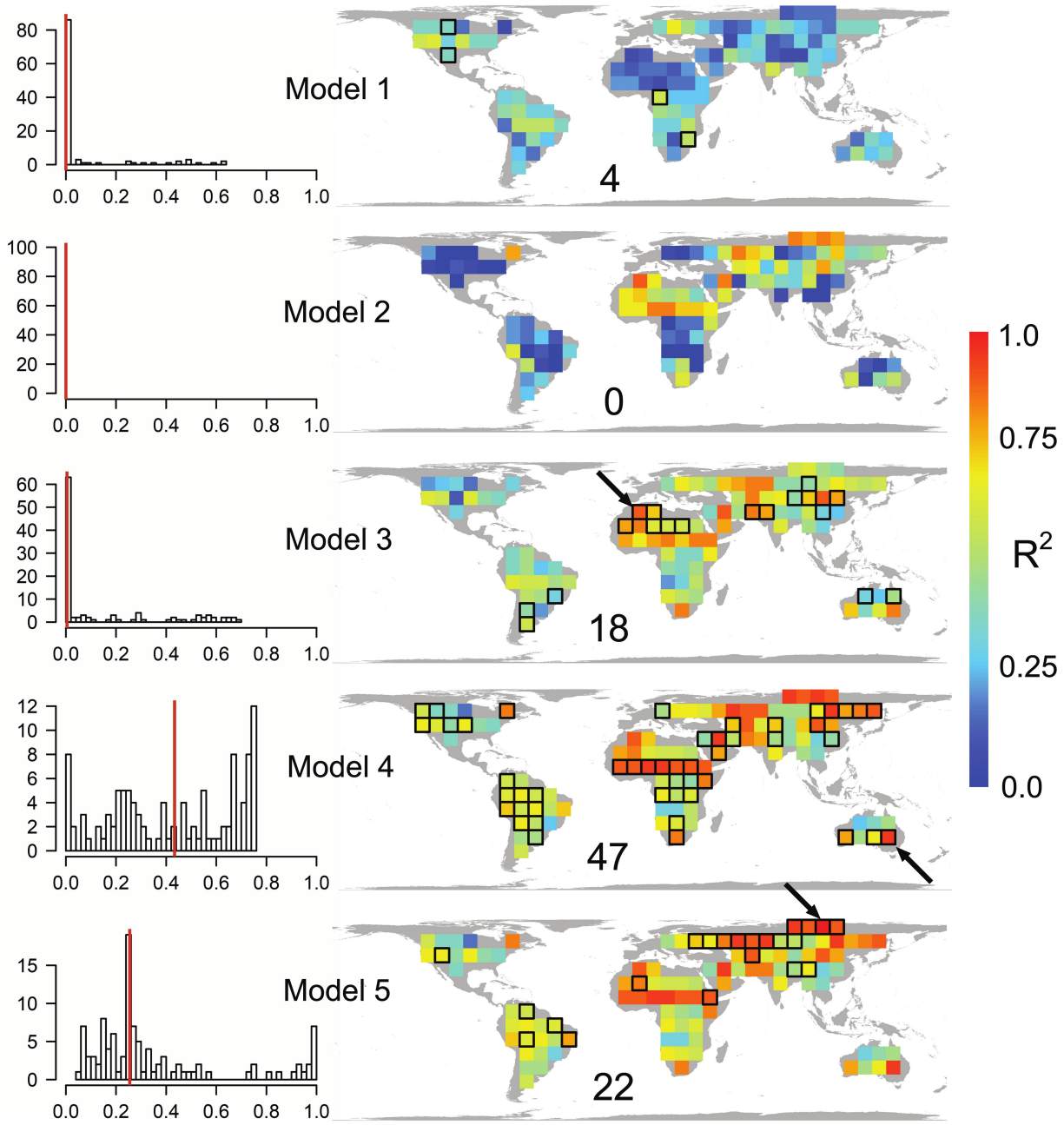

Figure 3: Histograms of model Akaike Information Criterion weights, with median values indicated by red bars. Maps depict spatial variation in the coefficient of determination (R^2) for each of the five models examined, and all maps use the same color scale. For each model, boxes highlight the regions for which the Akaike weight is >0.5, and the number of such regions is reported on each map. Arrows indicate the locations of the examples shown in figure 2.

lationships varied substantially among regions across the globe (fig. 4). Species-area slopes were highest across northern Africa, the Middle East, and the Himalayas, and there were several high values in regions spanning the Andes in South America. However, it is important to note that the regions with the highest species-area slopes were often poorly fitted by simple species-area relationships (cf. figs. 3 and 4). The highest values of species-mean NPP slopes were scattered across parts of South America and Asia. The five regions with the lowest species-mean NPP

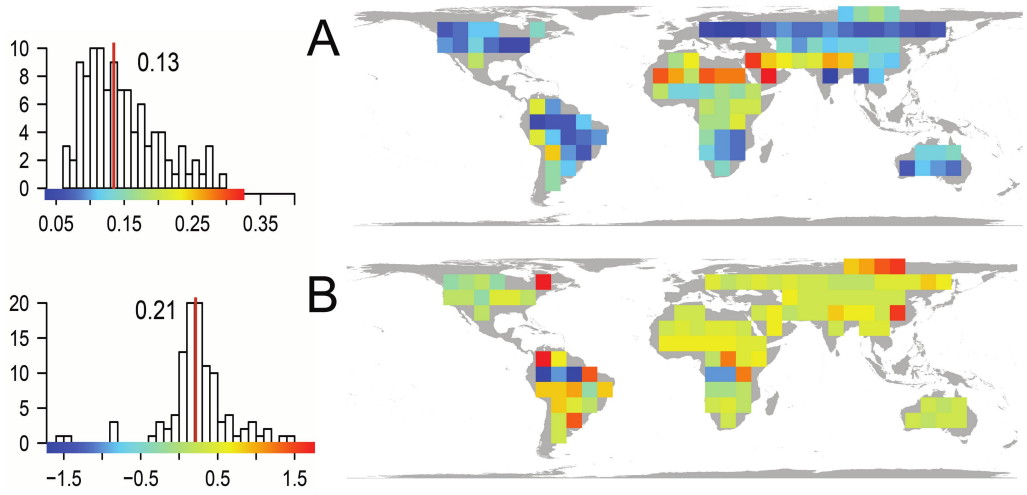

Figure 4: Parameter estimates from model 4 for species-area slopes (*A*) and for species-mean net primary production (NPP) slopes (*B*) are shown as histograms and mapped spatially. Red lines and numerical values on the histogram indicate the medians. The spatial variation in species-area and species-mean NPP slopes shown here are nearly identical to those obtained from univariate models 1 and 2 ($r = 0.962$ and $r = 0.997$, respectively).

slopes (ranging from −1.51 to −0.80) occurred in the Amazon and Congo river basins, often including a ridge of anomalously high richness values in the cells spanning the actual river courses (zip file). These five outliers (the rest of the species-mean NPP slopes ranged from −0.32 to 1.43) were excluded from analyses that attempted to explain variation in slopes (below). With the exception of these five regions, low species-mean NPP slopes occurred in western North America, western Australia, and parts of sub-Saharan Africa, all regions that were poorly fitted by model 2 (cf. figs. 3 and 4).

Predictors of Slope Variation

Species-area and species-mean NPP slopes varied substantially across the globe, and we examined the extent to which slopes estimated in model 4 could be explained by environmental attributes of regions (fig. 5; appendix). Regional species-area slopes were steeper in regions that had a large intraregional NPP range ($r_s = 0.55$, $P < .0001$). They were also much higher in regions that exhibited a steep within-region increase of land cover types with area (a steep habitat-area slope; $r_s = 0.54$, $P < .0001$). Species-area slopes decreased with a region's increasing average vertical habitat complexity ($r_s = -0.49$, $P < .0001$) and mean NPP ($r_s = -0.37$, $P < .0001$) and were more weakly correlated with the elevational range ($r_s = 0.30$, $P = .002$) and the number of biomes ($r_s = -0.33$, $P = .001$). Variation in species-area slopes was highly predictable, with 58% explained by this suite of six variables (appendix). A number of the variables were strongly collinear: most notably, regions with high mean NPP tended to have high vertical complexity and low NPP range and habitat-area slopes (appendix). Despite this collinearity, each environmental variable uniquely explained 2%–8% of the variance in species-area slopes after all other variables were entered. In addition, the model that included all six variables was identified as the best candidate model of the full suite of 63 possible models (Akaike weight = 0.66; appendix). In contrast, species richness–mean NPP slopes showed much weaker associations with the same variables (fig. 5; appendix), and only 17% of the variation in species-mean NPP slopes can be explained by this set of variables. The strongest univariate correlation was a positive relationship with mean NPP ($r_s = 0.20$, $P = .044$), while intraregional variation in NPP was only weakly correlated with species-mean NPP slopes ($r_s = -0.08$, $P = .40$; appendix). Both species-area and species-mean NPP slopes were positively correlated with the intraregional range in species richness among 1 × 1 cells (appendix). Other characteristics of the spatial distributions of both richness and NPP must be important to fully understand variation in species-mean NPP slopes.

Occupancy

Theory predicts that species-area slopes should be linked directly with values of mean occupancy within a region (Šizling and Storch 2004). We found a strong relationship between the two ($r_s = -0.95$), but species-area slopes tended to be lower than the theoretically predicted values (fig. 5). This suggests that the observed species-area re-

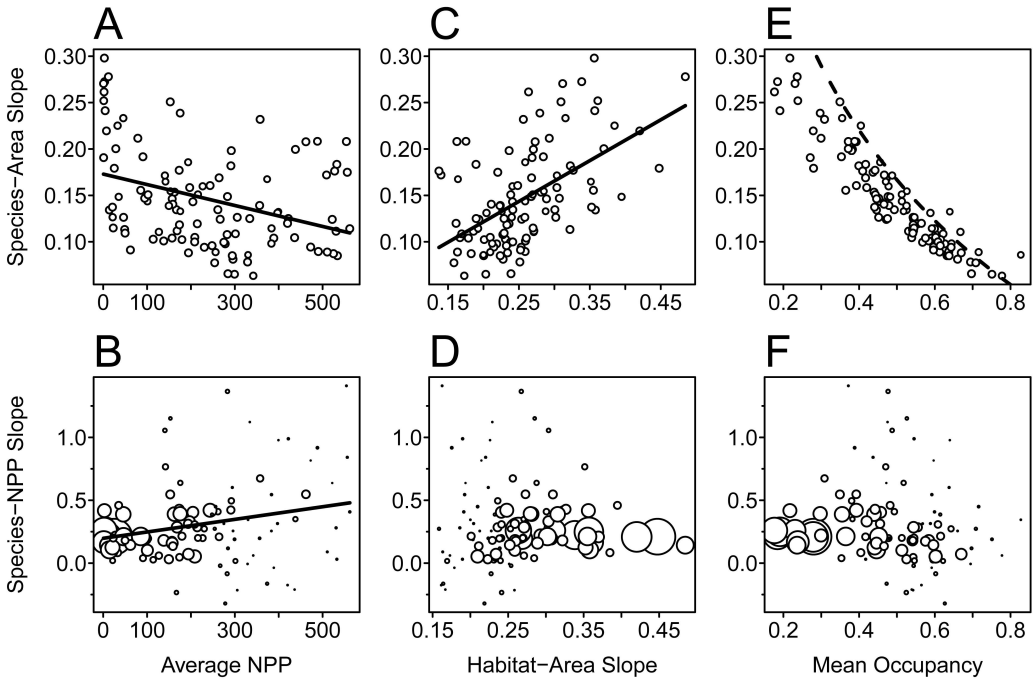

Figure 5: Scatter plots illustrating the relationship between species-area slopes (*A*, *C*, *E*) and species-energy slopes (*B*, *D*, *F*) as estimated by model 4 and the mean net primary productivity (NPP), the habitat-area slope (see text), and the mean species occupancy across all 107 regions. Five regions were excluded as outliers from species-energy slope plots (see text). Symbol size is inversely proportional to the standard error of the slope estimate. In *A*–*C*, lines illustrate regression models. In *E*, the dashed line represents the theoretical expectation between mean occupancy and species-area slopes.

lationships may deviate from a true power law, as has been commonly observed over certain spatial scales (Rosenzweig 1995; Šizling and Storch 2004). Occupancy also seemed to be important for determining which species-area-energy model was best supported in a region. Regions with the most support for model 3 tended to have the lowest values for mean species occupancy (fig. 6*A*). Regions in which fine-scale occupancy varied more strongly with NPP as measured by R^2 tended to exhibit greater support for model 5 (fig. 6*B*). Furthermore, the sign of the interaction term in those regions that had majority support for model 5 was generally opposite that of the occupancy-NPP relationship as predicted (fig. 6*C*).

Discussion

Ours is the first study to assess the degree to which area and energy availability have equivalent effects on continental species-richness patterns at a global extent. While Wright's (1983) model of area-energy equivalence almost always outperformed simple species-area or species-mean NPP relationships, we find that it was generally inferior to more complex models that allowed richness to increase at different rates with area and NPP. This finding is in general concordance with the few studies that have examined this issue over smaller regional extents (Storch et al. 2005, 2007) or other geographical subsets (Wylie and Currie 1993). However, while these studies each documented a difference in area and energy slopes, they did not interpret the difference in any mechanistic way. Storch et al. (2007) cautiously suggested that a difference would be interpretable only if "the measure of productivity was exactly proportional to abundance (in the same way as area), which is doubtful" (p. 316). Interpreting the difference in slopes is indeed difficult, and yet it is the exploration of this difference and why it might arise that may yield crucial insight into the drivers of species richness.

Energy versus Area Slopes

Interpretations of the differences in slopes fall under two basic categories. In the first, purely individual-based hypotheses for species richness, which are predicated on area-energy equivalence, are still retained, and the difference in observed slopes is attributed to systematic biases in our measurements of the relevant variables. First of all, any estimate of NPP is likely not a perfect measure of local

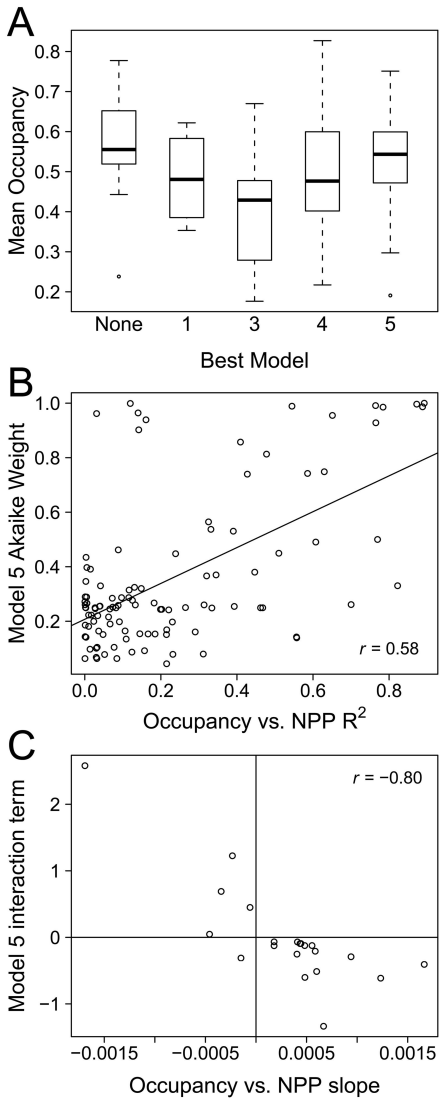

Figure 6: *A*, Box plots of mean occupancy values across regions grouped by the best fit species-area-energy model (ANOVA: $F_{4,102} = 4.57$, $P = .002$). *B*, Relative support for model 5 within a region as measured by the Akaike Information Criterion weight as a function of the strength of that region's relationship between mean occupancy and net primary productivity (NPP). *C*, The estimate of the interaction term in model 5 is negatively correlated with the slope of the occupancy-NPP relationship. One data point (from the western Sahara) was excluded as an outlier.

NPP, and systematic biases (e.g., at fine grains, between habitats) may exist. However, beyond this methodological caveat, in the quote above Storch et al. (2007) are suggesting that while $N \sim \overline{E}A$, the measure of $\overline{E}$—in our case, NPP—is nonlinearly related to $\overline{E}$; that is, $\overline{E} \sim \text{NPP}^k$. As a result, $N \sim \text{NPP}^k A$, and substituting into the relationship between richness and abundance expected from a log-normal abundance distribution, $S \sim N^z$, yields different expected slopes for the species-area and species-NPP relationships as $S \sim \text{NPP}^{kz}A^z$. This is an important consideration in that an implicit assumption in these sorts of broadscale macroecological studies is that the fraction of NPP available to the taxon of interest is relatively constant along the NPP gradient (i.e., $k = 1$). However, in order to explain the higher species-energy slopes as compared with species-area slopes in our data and those of Storch et al. (2005) and Wylie and Currie (1993), k must be greater than 1 (and on the order of $0.24/0.15 = 1.6$), meaning that along the NPP gradient, the energy available to birds increases disproportionately. While possible, the opposite is in fact more likely to be true given that amphibian, reptile, and to some extent mammal richness all increase at a faster rate than does avian richness over broad climatic or latitudinal gradients (Currie 1991; Qian and Ricklefs 2008).

The second category of interpretations regarding the area-energy slope difference assumes that the difference is not accounted for by potential biases in the energy-individual relationship. We have noted that in a pure Wrightian framework, area and energy affect richness via abundance as $S \sim N^z \sim (\overline{E}A)^z$; however, now let us assume that energy and area might additionally affect species richness in ways that are independent of abundance and that those effects are also well characterized by power laws: $S \sim (\overline{E}A)^z \overline{E}^{\alpha} A^{\beta}$ or $S \sim \overline{E}^{z+\alpha} A^{z+\beta}$. One obvious aspect of area that might lead to increases in species richness independently of the number of individuals is habitat diversity (Williams 1964; Rosenzweig 1995), and a number of recent studies have attempted to unite area per se and habitat diversity in statistical richness models (Triantis et al. 2003, 2005; Kallimanis et al. 2008). Habitat diversity may contribute to the intraspecific aggregation of individuals, which tends to steepen the slope of species-area relationships relative to those in which individuals are distributed randomly (He and Legendre 2002; Green and Ostling 2003). In particular, Kallimanis et al. (2008) found evidence for their model in which habitat diversity can affect the shape of the species-area slope (albeit of a Gleasonian exponential rather than an Arrhenius power form), and so we may consider that β is best interpreted as the effect that habitat diversity and/or spatial aggregation has on species richness mediated through area even though we are not actually able to separate β from z with our data. While we cannot estimate z, α, and β without data on abundances, a comparison of the empirically observed area and energy slopes indicates that α is clearly greater than β. This then begs the question: what aspects of the global terrestrial NPP gradient allow richness to increase at a rate that is 1.5 to two times faster than the increase with area due to habitat diversity and associated factors? The more-specialization hypothesis (Abrams 1995; Srivastava and

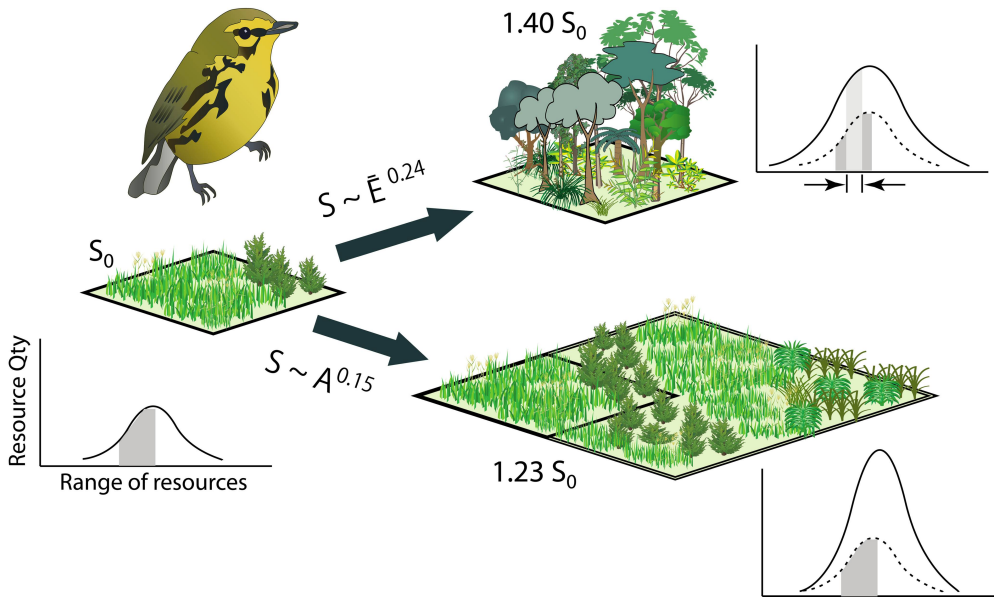

Figure 7: Illustration of the ways in which variation in area (A) and mean energy availability ($\overline{E}$) may differentially affect consumer species richness (S). The exponents shown are the mean regional estimates derived from this study that show the proportional effect of a fourfold increase in A or $\overline{E}$. A fourfold increase in $\overline{E}$ will tend to increase both the breadth of resource types available and the amount of energy available over any particular portion of the resource spectrum. On each resource distribution, the shaded area denotes an example of the range of resources required to support a minimum viable population. In the high-productivity environment, a population could specialize on a narrower range of resources and still support a minimum viable size. A fourfold increase in area may lead to the inclusion of previously unrecorded habitat and resource types, but the primary effect will be to increase the total amount of energy available over the preexisting resource spectrum. Because the extent to which individuals can specialize depends on resource density (as reflected by the dashed line) rather than total resource availability over some large area, if home ranges are typically much smaller than the region in question then mean niche breadth is expected to be similar in regions of similar resource density, regardless of area. This difference in the horizontal and vertical rates at which new ecological opportunities become available, together with constraints imposed by potential home range sizes, may explain why species-energy slopes tend to be greater than species-area slopes.

Lawton 1998; related to the niche-position hypothesis of Evans et al. 2005) suggests that as productivity increases, more specialist species are able to persist because of the greater number of resource types that provide at least some minimum energy requirement. Both vertical vegetation structure and complexity and plant species richness (Francis and Currie 2003; Kreft and Jetz 2007) increase along the global energy gradient ($r = 0.63$ at the regional level; appendix), and thus it is easy to imagine higher resource diversity in high-energy regions. The relationship between measures of vegetation structure and bird diversity has long been recognized (e.g., MacArthur and MacArthur 1961), and it has been shown to arise from the sequential addition of foraging guilds rather than through the expansion of guilds that are already present (Willson 1974). More recently, Hurlbert (2004) used rarefaction curves to show that for North American birds, structurally more complex environments supported more species than was expected on the basis of the number of individuals sampled. Jetz et al. (2009) also found strong associations between plant and vertebrate diversity at global scale, but they noted that at coarse-grained scales these may be difficult to disentangle from environmental correlates.

These results are consistent with an effect of productivity on species richness mediated by niche diversity, but why should this effect be stronger than the effect of area mediated by habitat diversity? We identify three possibilities. First, novel ecological opportunities arise more quickly with NPP than with area. Consider the following foraging guilds that might occur in a patch of grassland: omnivorous ground gleaner, low-foliage gleaner, and insectivorous sallier. If this patch is expanded in area by four times (within a region of roughly constant energy availability, for example, within a biome), then the same basic niches will be available, with the possible addition of others if the areal expansion included novel vegetation or habitat (fig. 7). Conversely, compare the number of available niches in the small grassland patch with those in a patch of equal area but with four times the energy availability. Such an increase in NPP will typically occur in conjunction with new strata of vegetation, and as such we may add middle- and high-canopy gleaners and salliers, bark glean-

ers, and bark drillers (Willson 1974; Holmes et al. 1979); thus, the potential resource distribution is wider (fig. 7). Although it is not necessarily the case in aquatic or marine systems, where increases in NPP often result in dominance by a few plankton species and little change in the structural complexity of the system, global terrestrial NPP gradients usually encompass a gradient of novel ecological opportunities for consumers.

Second, higher resource density allows for increased specialization along a resource axis while still maintaining some minimum viable population size (fig. 7; MacArthur 1972; Pianka 2000). While a larger area also includes a greater amount of resources that could theoretically be subdivided more finely, specialization occurs at the level of the individual (Bolnick et al. 2003) and limits on home-range size (e.g., Hixon 1980) will prevent any individual from experiencing the total resources available over a large area. For example, the total amount of resources available within a 100-km^2 region is largely irrelevant to an individual with a home range of 0.2 ha. As such, increases in area are not expected to facilitate resource specialization as much as increases in resource density are.

Third, Allee effects will be greater in a larger area relative to in a smaller area given equal total resources. If areas A and B can both support 10 individuals but area A is 1 ha while area B is 1 km^2, then individuals in area B may have greater difficulty in encountering mates, maintaining antipredator vigilance, and cooperatively defending resources, among other potential issues related to Allee effects (Stephens et al. 1999). Such Allee effects are expected to be ameliorated with increases in mean energy availability that allow subsequent increases in population density, while increases in area alone would have no effect on mean population density.

Understanding Geographic Variation in Model Performance and Slopes

While species-energy slopes are generally steeper than species-area slopes, substantial geographic variation exists in them. Species-area slopes can be analytically related to measures of turnover, beta diversity, and occupancy (Harte and Kinzig 1997; Šizling and Storch 2004; Tjørve and Tjørve 2008), and as such, within regions of high species-area slope, species turn over in space more rapidly, subregions exhibit higher beta diversity, and species on average occur over a smaller fraction of the landscape. It is therefore of no surprise that variables related to the heterogeneity of the environmental template, such as elevational range, habitat diversity, and the habitat-area slope, together explained more than half (53%, compared with 58% for the full six-variable model) of the variation in species-area slopes. In regions of high environmental heterogeneity and low occupancy, the rate at which richness increased with area was more likely to be similar to the rate at which richness increased with energy. It is important to note that our analyses were conducted over arbitrarily defined regions. By examining more homogeneous and biogeographically relevant regions, mean occupancy might be greater and the nonequivalence of area and energy slopes might be potentially more pronounced. Furthermore, we have examined species-area-energy relationships only within nested regions, although preliminary nonnested analyses suggest qualitatively similar results (A. H. Hurlbert and W. Jetz, unpublished data).

In some regions, the best-supported species-area-energy model was the one that included an interaction term that allowed the species-area slope to vary with energy and vice versa. This implies a curved surface when plotting log S as a function of log A and log $\overline{E}$, as opposed to a flat plane as envisioned by Wright's (1983) power law–based framework of area-energy equivalence. Twenty of the 22 regions that were best fitted by this model exhibited asymmetric effects of area and energy, as reflected in the relative support for models 3 and 4 (appendix). There has been some debate recently regarding the nature of this interaction, primarily in the context of how species-area slopes vary with latitudinal or energetic gradients. A number of authors have documented a negative relationship between species-area slopes and latitude (Rodríguez and Arita 2004; Drakare et al. 2006; Qian et al. 2007) or a positive relationship between species-area slopes and climatic variables such as temperature and precipitation (Kalmar and Currie 2006, 2007); both of these relationships might be interpreted as support for a positive area-energy interaction. Others have documented—or their data exhibit—a negative area-energy interaction using estimates of NPP, vegetation indices, or latitude (Kaspari et al. 2000; Lyons and Willig 2002; Storch et al. 2005; Evans et al. 2008). As we show and as was noted by Storch et al. (2005, 2007), the expected sign of the area-energy interaction term will depend on how mean species occupancy (or conversely, mean species turnover) changes along the energy gradient. In regions where mean occupancy decreases with NPP and turnover increases, we found a positive interaction as expected. In these regions, the areas of highest NPP coincide with regions of high topographic relief or novel biomes where occupancy would be expected to be low (Hurlbert and White 2005, 2007).

More frequently in this data set, however, occupancy increased with NPP, leading to a negative interaction term when the interaction model received the most support. In a study of South African birds, Bonn et al. (2004) also found that occupancy increased along an energy gradient, and they interpreted this in the context of energy availability positively affecting the probability of persistence of

any species on average. In a related result, Evans et al. (2008) found that species turnover in British birds was lower in high-energy regions. The regions with the strongest negative interaction in this study were those that occurred at high latitudes across Eurasia (fig. 4). In these regions, not only is there a very simple north-south NPP gradient, but the nature of species distributions is strongly nested due to the overlay of range maps for species with variable northern extents (e.g., fig. 2*C*). Under a hypothetical scenario in which one species was added with each latitudinal band moving south, the difference between the two northernmost bands (one vs. two species) is proportionally much greater than the difference between the two southernmost bands (seven vs. eight species). This is another way of illustrating that when underlying species distributions are nested and coincide with an underlying NPP gradient, species turnover will decrease and mean occupancy will increase along that gradient. Despite finding majority support for the interaction model in only 22 (20.6%) of 107 of the regions examined, we did find a strong negative relationship globally between species-area slope and the average NPP of a region. The lack of identification of an area-energy interaction in many regions despite this global relationship may suggest that an interaction is evident only in the presence of sufficient variation in NPP.

Conclusions

The latitudinal gradient of species richness and the species-area relationship are two canonical patterns in ecology that share one class of hypotheses on the basis of the number of individual organisms that can be supported within a region. Although it is likely that several different classes of processes contribute to the observed complex global diversity patterns, a comparison of the rate at which species richness increases as a function of either area or energy is useful as a first step toward estimating the relative importance of those classes of explanation. In general, we find that richness increases faster with mean energy availability than it does with area, suggesting that individual-based hypotheses must be viewed as insufficient for explaining geographic patterns of species richness and that energy clearly has effects on richness above and beyond those expected on the basis of the number of individuals. As envisioned by Brown (1981), an understanding of division rules is at least as important as an understanding of capacity rules for fully explaining biodiversity patterns. We suggest that the more-specialization hypothesis—that higher resource density allows for increased specialization—merits further attention for explaining positive richness-productivity relationships at the global extent. Our study also illustrates how, by affecting the occupancy and distribution patterns of individual species, environmental variables are predictably related to species-area slopes and the nature of species-area-energy relationships. In addition to furthering our understanding of the relationship between the environmental template and various macroecological patterns, our results also have implications for how species-area relationships may find more sophisticated use in conservation.

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