Area–heterogeneity tradeoff and the diversity of ecological communities

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For more than 50 y ecologists have believed that spatial heterogeneity in habitat conditions promotes species richness by increasing opportunities for niche partitioning. However, a recent stochastic model combining the main elements of niche theory and island biogeography theory suggests that environmental heterogeneity has a general unimodal rather than a positive effect on species richness. This result was explained by an inherent tradeoff between environmental heterogeneity and the amount of suitable area available for individual species: for a given area, as heterogeneity increases, the amount of effective area available for individual species decreases, thereby reducing population sizes and increasing the likelihood of stochastic extinctions. Here we provide a comprehensive evaluation of this hypothesis. First we analyze an extensive database of breeding bird distribution in Catalonia and show that patterns of species richness, species abundance, and extinction rates are consistent with the predictions of the area–heterogeneity tradeoff and its proposed mechanisms. We then perform a metaanalysis of heterogeneity–diversity relationships in 54 published datasets and show that empirical data better fit the unimodal pattern predicted by the area–heterogeneity tradeoff than the positive pattern predicted by classic niche theory. Simulations in which species may have variable niche widths along a continuous environmental gradient are consistent with all empirical findings. The area–heterogeneity tradeoff brings a unique perspective to current theories of species diversity and has important implications for biodiversity conservation.

habitat heterogeneity | neutral theory | stochastic model of community dynamics | conservation planning

Area and environmental heterogeneity are two of the most fundamental determinants of species diversity (1). A large area is capable of supporting larger populations than a smaller area, thereby reducing the likelihood of stochastic extinctions (Fig. 1A, light blue ellipse). This paradigm is an essential element of metapopulation dynamics theory (2), island biogeography theory (3), and recent stochastic theories of species diversity (4, 5). Environmental heterogeneity (spatial heterogeneity in environmental conditions) is a crucial determinant of species diversity because a more heterogeneous area provides suitable conditions for a larger number of species with different ecological requirements, thereby increasing the effective species pool (Fig. 1A, orange ellipse). This mechanism is an essential element of niche-based theories of species diversity (6, 7). These complementary mechanisms constitute the heart of community ecology (8, 9) and have broad implications for biodiversity conservation planning (10–13).

Recently it has been demonstrated that these two fundamental mechanisms are inherently linked through a simple geometric constraint termed here "the area–heterogeneity tradeoff" (14, 15) (Fig. 1A, green ellipse). Specifically, unless niche width of all species is unlimited, any increase in environmental heterogeneity within a fixed space must lead to a reduction in the average amount of effective area available for individual species. The strength of this tradeoff is expected to increase with decreasing niche width of the relevant species because a narrower niche

increases the likelihood of stochastic extinctions (16) (Fig. 1B). Surprisingly, although the effects of area and heterogeneity on species diversity have been investigated and accepted for almost a century, the consequences of this fundamental tradeoff have been completely overlooked.

Here we provide a comprehensive evaluation of this tradeoff. Specifically, the area–heterogeneity tradeoff provides four testable predictions. First, species richness is expected to increase with increasing heterogeneity at relatively low levels of heterogeneity (when area is not a limiting factor), but to decrease above some critical threshold when area becomes a significant limiting factor. As a result, the general pattern of the heterogeneity–diversity relationship should be unimodal (Fig. 2A). Second, because niche width affects the sensitivity of species to the area–heterogeneity tradeoff (Fig. 1B), the position of the inflection point (the level of heterogeneity that maximizes richness) should depend on niche width of the component species. As a result, the number of species characterized by very narrow niches is expected to decrease over most values of increasing heterogeneity, whereas the number of species with very broad niches is expected to increase (Fig. 1B). Third, the reduction in the effective area with increasing heterogeneity should generate a negative relationship between environmental heterogeneity and average population size (Fig. 2B). Fourth, the reduction in population sizes should increase the probability of stochastic extinctions, leading to a positive effect of environmental heterogeneity on extinction rates (Fig. 2C).

We tested all four predictions using data on breeding bird distributions among Universal Transverse Mercator (UTM) grid cells of 10 × 10 km in Catalonia (17, 18) (SI Appendix). This system was ideal for our purposes because data on species composition in each grid cell were available for two distinct survey periods (1980–1982 and 1999–2003), and the second survey provided standardized estimates of individual species abundance and sampling effort (18). The data collected in the second survey also showed that elevation is a major determinant of bird distributions in this area and that different species show striking differences in both the position and the width of their "niches" along the elevation gradient (18). We therefore used elevation range as a measure of environmental heterogeneity in our analyses.

Consistent with the predictions of the area–heterogeneity tradeoff, elevation range had a significantly unimodal effect on species richness (Fig. 2D), a significantly negative effect on mean species abundance (Fig. 2E), and a significantly positive effect on
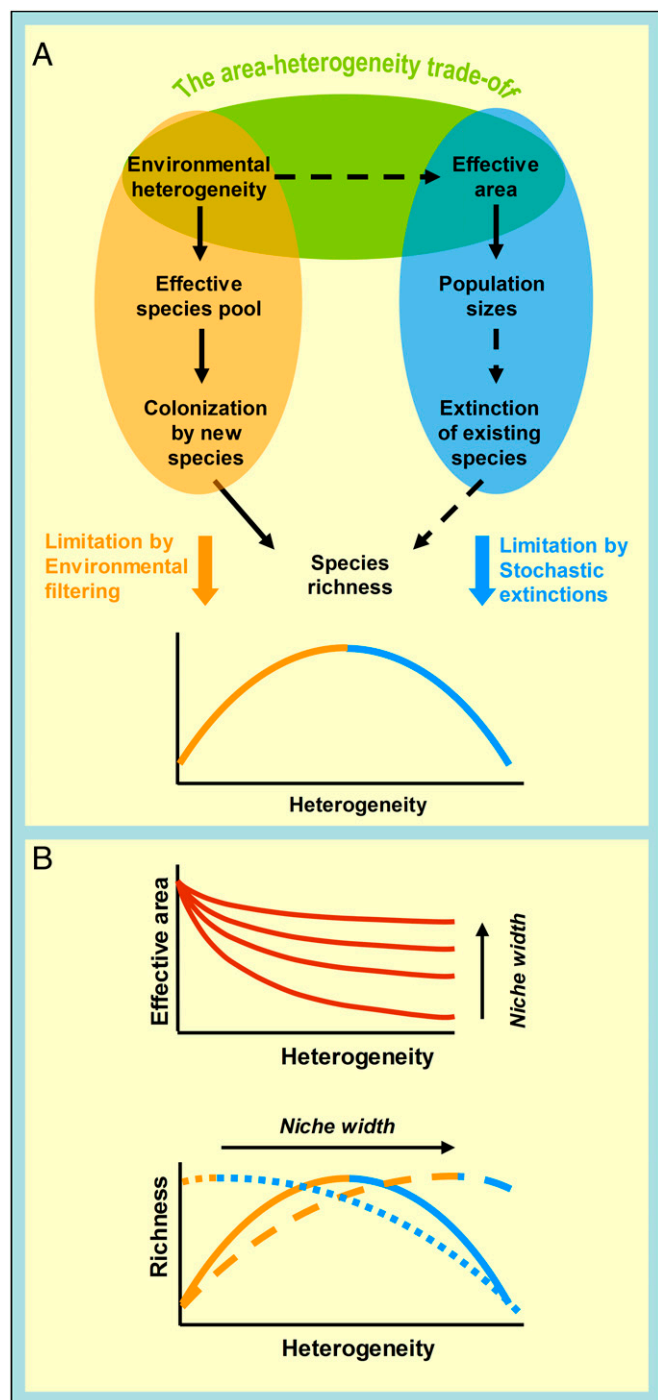
Fig. 1. Conceptual basis of the area–heterogeneity tradeoff. (*A*) A graphical model of the area–heterogeneity tradeoff. Solid arrows, positive effects; dashed arrows, negative effects. Increasing environmental heterogeneity increases the likelihood of successful colonization by providing suitable conditions to a larger number of species (orange ellipse) but increases the likelihood of stochastic extinctions by reducing the amount of effective area available for individual species (blue ellipse). These contrasting mechanisms combine to produce a general unimodal relationship between environmental heterogeneity and species richness, with uniform environments showing a decrease in richness due to deterministic processes (environmental filtering of species lacking adaptations to the relevant habitats) and highly heterogeneous environments showing a decrease in richness due to stochastic extinctions of species with low population sizes. (*B*) Effect of niche width on the response of effective area (*Upper*) and species richness (*Lower*) to environmental heterogeneity.

extinction rates (Fig. 2*F*). All of these patterns remained statistically significant after controlling for the effects of area, spatial autocorrelation, absolute elevation, mean annual temperature, mean annual rainfall, population density, and broad-scale spatial effects (*SI Appendix, SI Methods* and Tables S1–S3). The unimodal effect of heterogeneity on species richness was still significant after the removal of four possible outliers (the two right-most and two lowest points in Fig. 2*D*). Sampling effort had a statistically significant effect on species richness for both survey periods but did not affect the results of the analyses (*SI Appendix, SI Methods,* Figs. S1 and S2, and Tables S4–S6).

Although the response of overall richness to elevation range was significantly unimodal in all analyses (*SI Appendix,* Table S3), a stronger test of the area–heterogeneity tradeoff should focus on the response of species with different niche widths. Such differences affect the sensitivity of individual species to environmental heterogeneity and can therefore be important in determining the overall shape of the heterogeneity–diversity relationship (Fig. 2*B*). We tested the effect of niche width on the heterogeneity–diversity relationship by categorizing the species into four quartiles of niche width based on their elevational distribution in the study area (*SI Appendix*). As predicted, increasing niche width shifted the level of elevation range that maximized species richness to higher levels (Fig. 3*A*). Moreover, although quadratic models better fitted the data for all groups of species than linear models, piecewise linear regression models revealed that species with the smallest niche width (0–25% quartile) showed a monotonic decrease in richness with increasing elevation range ($t = -13.09$, $P < 0.0001$); for species classified into the second quartile (25–50%) only the decreasing phase of the relationship was statistically significant ($t = -11.205$, $P < 0.0001$); for species classified to the third category (50–75%) both the increasing and decreasing phases were statistically significant (increasing range: $t = 10.16$, $P < 0.0001$, decreasing range: $t = -3.65$, $P < 0.0001$); and for species with the largest niche width (75–100%) only the increasing phase was statistically significant ($t = 19.843$, $P < 0.0001$). All these patterns are consistent with the area–heterogeneity tradeoff. An important conclusion from these results is that heterogeneity–diversity relationships observed at the whole-community level are expected to depend on the distribution of niche width among the component species.

If the observed shift in the level of heterogeneity that maximizes species richness (Fig. 3) was caused by lower sensitivity of broad-niche species to stochastic extinctions, one would expect that increasing niche width would reduce the effect of elevation range on extinction probabilities. Further analyses (*SI Appendix,* Fig. S3) are consistent with this prediction and show that the effect of elevation range on extinction probabilities decreased with increasing niche width. This finding provides additional support to the area–heterogeneity tradeoff and confirms our hypothesis that the strength of this tradeoff decreases with increasing niche width (Fig. 1*A*).

Although all observed patterns fit the predictions of the area–heterogeneity tradeoff, alternative explanations cannot be ruled out (e.g., an increase in extinction rates due to higher disturbances in landscapes with high elevation range, or differences in the composition of the regional species pool among regions with different elevation ranges). To explore the generality of the area–heterogeneity tradeoff we performed a series of numerical simulations in which we tested the same predictions using a stochastic model of community dynamics (*SI Appendix*). These simulations also allowed us to get some idea about the "noise" expected in empirical tests of our predictions, an important question given that our results were very noisy (Fig. 2 *D–F*). In our model the environment was reduced into a single environmental factor *E*, and the niche of each species was described by a Gaussian response indicating the probability of establishment as a function of *E* (*SI Appendix, SI Methods* and Fig. S4). In this
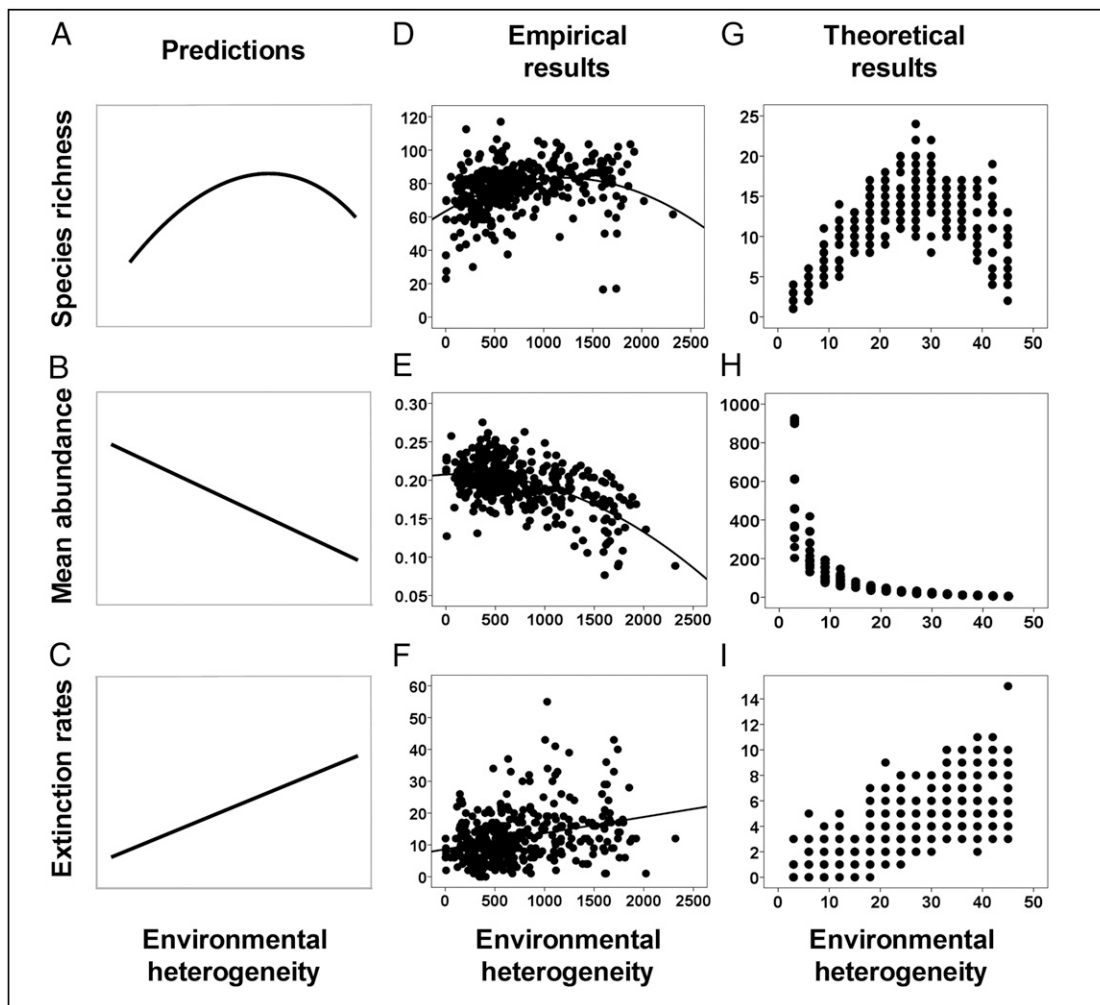
Fig. 2. Predicted, observed, and simulated responses of ecological communities to environmental heterogeneity. Predicted responses (*A–C*) are based on the graphical model of the area–heterogeneity tradeoff (Fig. 1). Empirical responses (*D–F*) are based on the analysis of breeding bird distribution in Catalonia with elevation range as a measure of environmental heterogeneity (*SI Appendix*). All patterns were statistically significant and robust to the effects of other, potentially confounding factors (*SI Appendix*, Tables S1–S3). Simulated responses (*G–I*) are based on the analysis of a spatially implicit, stochastic model of community dynamics (*SI Appendix*). Each dot represents a single realization to visualize the amount of noise expected in empirical data due to pure demographic stochasticity. In all simulations *A* (area) = 1,000, *R* (reproduction) = 45, *M* (mortality) = 1, *I* (immigration) = 0.2, and σ (niche width) = 2.

formulation the range of *E* represents the degree of environmental heterogeneity, and the SD of the species response is a measure of niche width (19). This formulation differs from our original model, whereby each species had a single source habitat (14), and allows incorporating differences in species' niche widths along a continuous environmental gradient.

Consistent with our empirical findings, increasing environmental heterogeneity had a unimodal effect on species richness, a negative effect on average population size, and a positive effect on extinction rates (Fig. 2 *G–I*). All these patterns were robust to variations in the demographic parameters (*SI Appendix, SI Methods* and Figs. S5 and S6). Moreover, according to the model, increasing niche width shifts the level of heterogeneity that maximizes species richness to higher levels (*SI Appendix*, Fig. S8), as found in our empirical analysis (Fig. 3*A*). These theoretical findings strength the theoretical basis of the area–heterogeneity tradeoff and support its proposed mechanisms. The results also show that, even at the absence of any other deterministic or stochastic effects, pure demographic stochasticity may introduce considerable noise to empirical tests of our predictions (Fig. 2 *G–I*). This result is important because ecologists studying patterns of species diversity tend to ignore the

inherent noise expected from demographic stochasticity and often attribute low values of R^2 to the effect of "hidden" variables not included in the analysis.

Although the global shape of the heterogeneity–diversity relationship is predicted to be unimodal, *specific* systems are predicted to show positive, negative, unimodal, or flat responses, depending on properties of the species and the spatiotemporal scales of the analysis, both of which affect the position of the inflection point (the level of heterogeneity that maximizes species richness). For example, species with high reproduction rates and species with wide niches are expected to show predominantly positive responses (*SI Appendix*, Figs. S5*C* and S8), whereas species with very narrow niches are expected to show a predominantly negative response (*SI Appendix*, Fig. S8). Scale also matters. According to our simulations increasing area may change the shape of the relationship from unimodal to positive without any change in the demographic parameters (*SI Appendix*, Fig. S7*A*). Increasing the temporal extent of data collection has a similar effect (*SI Appendix*, Fig. S7*B*). It can therefore be expected that natural communities would show variable heterogeneity–diversity relationships, depending on properties of the species, the environment, and the scales of the analysis. Empirical
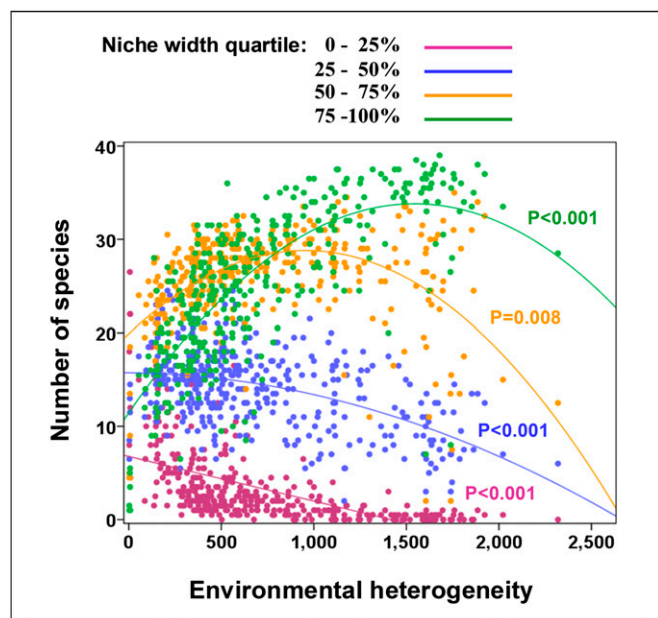
Fig. 3. Effect of niche width on the response of species richness to environmental heterogeneity based on the analysis of breeding bird distribution in Catalonia with elevation range as a measure of heterogeneity (*SI Appendix*). Each color represents a different quartile of niche width. Increasing niche width shifts the level of elevation range that maximizes species richness to higher levels. *P* values indicate significance levels in the regression models.

evidence supports this prediction and shows that the qualitative shape of the heterogeneity–diversity relationship may vary among different groups of organisms in the same region (20), within the same group of organisms among different regions (21), and within the same group of species and the same region when the data are analyzed at different scales (22). Furthermore, Tamme et al. (23) recently showed that negative effects of habitat heterogeneity on species richness are significantly more common at small spatial scales, a finding fully consistent with our simulations (Fig. 4A).

Although positive heterogeneity–diversity relationships are documented much more frequently than negative or unimodal relationships, this evidence may suffer from at least three sources of bias. First, in many studies, particularly at large geographical scales, estimates of species richness are based on spatial interpolation, range maps, or ecological niche models (24–26). Clearly, such analyses are not expected to show evidence for stochastic extinctions. Estimates of species richness based on data collected over long time periods [e.g., herbaria and museum collections (27, 28)] are also biased because colonization events are accumulated over time, whereas extinction events are ignored. Our simulations show that this source of bias may eliminate the stochastic extinction signal (*SI Appendix*, Fig. S7B).

Third, much evidence for positive heterogeneity–diversity relationships comes from studies focusing on insular systems. Such evidence might be biased owing to underlying correlation between island area and the degree of environmental heterogeneity. Although models focusing on such systems often test the combined effects of area and heterogeneity, such models are rarely designed to account for possible unimodal heterogeneity–diversity relationships. To assess the potential consequences of such bias we performed a metaanalysis of heterogeneity–diversity relationships using 54 published datasets for which data on area, elevation range, and species richness were available (*SI Appendix*). Statistically significant positive effects of elevation range on species richness were documented for 43 of these

datasets (*SI Appendix, SI Methods* and Table S7). However, once the effect of area was adjusted for, only six of these patterns remained significantly positive (Fig. 4A). The majority of the remaining patterns become significantly unimodal (14 patterns) or nonsignificant (20 patterns; Fig. 4A). The mean effect size of the quadratic response calculated for all 43 area-corrected models was significantly lower than zero, consistent with the prediction of the area–heterogeneity tradeoff (*SI Appendix*). A corresponding analysis based on 18 datasets for which data on habitat diversity were also available revealed results similar to those obtained for elevation range ($\kappa = 0.68$, $n = 18$, $P < 0.001$; Fig. 4 B–F). These overall results strongly support the hypothesis that the general relationship between species richness and environmental heterogeneity is unimodal.

Recognizing the potential consequences of the area–heterogeneity tradeoff is crucial for biodiversity conservation. On the basis of the assumption that environmental heterogeneity increases species diversity, it is often proposed that highly heterogeneous areas should receive a higher priority for conservation than less heterogeneous areas (29, 30) and that management actions should be targeted at increasing the heterogeneity of habitat conditions as a means for promoting local species diversity (12, 31). Our findings demonstrate that such decisions may lead to unintended results, particularly if the overall size of the protected area is small and population sizes are already small, as often is the case.

In summary, the concept of the area–heterogeneity tradeoff (Fig. 1) adds a unique perspective to current theories of species diversity by demonstrating that increasing environmental heterogeneity may reduce species richness by increasing the likelihood of stochastic extinctions. The agreement between our theoretical and empirical findings supports this idea and shows that this tradeoff may influence a variety of population-level and community-level processes. The area–heterogeneity tradeoff provides a mechanistic link between the fundamental elements of niche theory and island biogeography theory and is fully consistent with the growing recognition that both deterministic and stochastic processes are important in determining the diversity of ecological communities (14, 19, 32). Furthermore, if the functional relationship between environmental heterogeneity and species richness is determined by the balance between deterministic and stochastic drivers of species richness (Fig. 1B), empirical analyses of this relationship provide a possible clue for assessing the relative importance of deterministic vs. stochastic drivers of species diversity, a central question in contemporary ecology (14, 19, 32, 33).

Methods

SI Appendix, SI Methods provides a full description.

Empirical Analyses. We used data on breeding bird distributions in Catalonia (northeast Spain) collected in two distinct surveys, 1975–1982 (17) and 1999–2002 (18), in the same set of 372 observation units (UTM grid cells of 10 × 10 km or smaller, irregular polygons in the case of border or coastal grid cells), covering 99% of the terrestrial area of Catalonia. We determined elevation range at a radius of 7 km around the center of each polygon. Radii of 10 km and 14 km showed high correlation (Pearson correlation = 0.93–0.97) and had similar effects on species richness. Extinction rates for each cell were estimated as the number of species that were present in the first survey but not in the second survey. We used ordinary least squares (OLS) regression to analyze the effect of elevation range on mean species abundance, extinction rates, and species richness, using a linear and squared term of elevation range. In further analyzes, we constructed more complex OLS models incorporating the effects of area, mean absolute elevation, mean annual rainfall, mean annual temperature, human population density, and broad-scale spatial effects to evaluate the robustness of the patterns to other, potentially confounding factors that might influence the dynamics and structure of the study species. We also performed the analysis correcting for spatial autocorrelation using conditional autoregressive regression and simultaneous autoregressive regression models (34). Niche width of each

Fig. 4. Effect of area correction on the relationship between species richness and environmental heterogeneity. (*A*) Functional relationships between species richness and elevation range after correcting for the effect of area in 43 datasets for which an initially uncorrected (linear) model revealed significantly positive effect of elevation range on species richness. (*B*) Correspondence between the effects of elevation range and habitat diversity on species richness based on 18 datasets for which data on both variables were available ($\kappa = 0.68$, $P < 0.0001$). (*C* and *D*) Effect of elevation range on bird species richness in the Lesser Antilles (20). Results are shown for analyses performed before (*C*) and after (*D*) correcting for the effect of area by taking the residuals of both factors over area. (*E* and *F*) A similar comparison but with habitat diversity as a measure of environmental heterogeneity. For both measures of heterogeneity the uncorrected effect of heterogeneity on species richness was significantly positive (*C* and *E*), but once both richness and heterogeneity were corrected for the effect of area, the relationship turned out to be significantly unimodal (*D* and *F*).

species was determined according to its distribution along the elevation gradient (difference between maximum and minimum elevation after removal of outliers). We then categorized the species into four "niche quartiles" and regressed the number of species belonging to each niche quartile against elevation range and its squared value.

Theoretical Analyses. We used a stochastic, individual-based, spatially implicit model of a local community that receives immigrants from a regional species pool with *N* species. The dynamics were modeled as a continuous-time Markov process, whereby individuals go through the fundamental demographic processes of reproduction, mortality, and migration, all modeled with explicit rates, constant among species. The landscape consists of *A* sites, where each site can be occupied by at most one individual. Environmental heterogeneity is introduced by assigning each site an environmental value that is randomly drawn from a uniform distribution. The range of *E* available for the local community represents the degree of environmental heterogeneity. This range is embedded within a larger range representing the range of *E* in the area available for the regional species pool (*SI Appendix,* Fig. S4). A new offspring is immediately dispersed into a random site. The niche of each species along the environmental gradient is described by a Gaussian function indicating the probability of establishment at empty sites as a function of *E*, normalized to ensure that all species are equivalent

in their overall probability of establishment within the regional environmental range. Individuals arriving in occupied sites die without being able to establish.

Metaanalysis. We compiled a database of 54 species-island systems with information on elevation range, area, and species richness. We regressed elevation range against area and log species richness against log area. We then regressed the residuals of species richness over area against the residuals of elevation range over area using both linear and quadratic regression models and compared the results obtained for the quadratic vs. linear models using the sample size-corrected Akaike Information Criterion. We also calculated the average effect size of all area-corrected quadratic models according to their *F* values, to more formally test for the prevalence of unimodal relationships. We classified the patterns as unimodal, U-shaped, positive, negative, or nonsignificant according to the criteria in *SI Appendix, SI Methods, C.4*.

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