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# Reconciling topographic and climatic effects on widespread and range-restricted species richness

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## ABSTRACT

**Aim** To identify the reasons behind differing geographical species richness patterns of range-restricted and widespread species.

**Location** The Western Hemisphere.

**Methods** We used regression to determine the strongest environmental predictors of richness for widespread and range-restricted mammal species in 10,000 km<sup>2</sup> quadrats in the continental Americas. We then used range-placement models to predict the expected correlation between range-restricted and widespread species richness were they to be determined by identical, random, or contrasting environmental factors. Finally, to determine the reasons underlying deviations from these predictions, we divided the Americas into 5% quantiles based on temperature and topographic heterogeneity and correlated richness of these two assemblages across quantiles – an approach that avoids constraints on statistical testing imposed by low potential for range overlap among range-restricted species.

**Results** Minimum annual temperature was the strongest predictor of widespread species richness while topographic heterogeneity was the best, although weak, predictor of range-restricted species richness in conventional regression analysis. Our models revealed that the observed correlation between range-restricted and widespread species richness was similar to what would be observed if both range-restricted and widespread species richness were determined by temperature. Patterns of range-restricted and widespread species richness were highly correlated across temperature quantiles, but range-restricted species uniquely showed an increasing pattern across heterogeneity quantiles.

**Main conclusions** Species richness gradients among range-restricted species differ from those of widespread species, but not as extensively or for the reasons reported previously. Instead, these assemblages appear to share some but not all underlying environmental determinants of species richness. Our new approach to examining species richness patterns reveals that range-restricted and widespread species richnesses share a common response to temperature that conventional analyses have not previously revealed. However, topographic heterogeneity has assemblage-specific effects on range-restricted species.

## Keywords

**Climatic gradients, range-restricted species, range size, species richness gradients, topographic heterogeneity, widespread species.**

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## INTRODUCTION

Many studies have shown that species richness patterns of widespread and range-restricted species differ substantially. This pattern has been documented globally (Orme *et al.*, 2005;

Ceballos & Ehrlich, 2006; Grenyer *et al.*, 2006; Lamoreux *et al.*, 2006) and within individual biogeographical domains (Jetz & Rahbek, 2002; Lennon *et al.*, 2004; Ruggiero & Kitzberger, 2004; Vázquez & Gaston, 2004; Evans *et al.*, 2005; Kreft *et al.*, 2006; Rahbek *et al.*, 2007). While climate has been strongly linked to

broad-scale species richness patterns (Hawkins *et al.*, 2003), studies considering how range size affects climate–richness relationships consistently show that climate predicts much of the variation in widespread species richness but is of little importance for patterns of range-restricted species richness (Jetz & Rahbek, 2002; Evans *et al.*, 2005; Kreft *et al.*, 2006; Rahbek *et al.*, 2007). These spatial trends appear robust temporally: species' responses to climate change are more readily detectable among widespread than range-restricted species (Menendez *et al.*, 2006; White & Kerr, 2006). Conversely, several studies have identified topographic heterogeneity as being disproportionately important as a determinant of range-restricted species richness (Jetz & Rahbek, 2002; Kreft *et al.*, 2006; Rahbek *et al.*, 2007).

Understanding these differences between range-restricted and widespread species is of fundamental importance for macroecological research, but also for its global change applications. Previous studies have generally interpreted weak correlations between range-restricted species richness and climate as indicating that although climate is a strong determinant of richness among widespread species it is a minor determinant for range-restricted species (Jetz & Rahbek, 2002; Evans *et al.*, 2005; Kreft *et al.*, 2006; Rahbek *et al.*, 2007). If true, this finding implies that many of the mechanisms that have been proposed to explain diversity gradients are only applicable to widespread species. In addition, if climate has little influence on species richness for range-restricted species, then expectations of their risk of extinction as a result of climate change might require global reassessment.

Richness gradients among widespread and range-restricted species may differ because of differences in the underlying environmental determinants of each gradient or as a consequence of differences in the intrinsic capacities of these assemblages to form spatial gradients (or both). To detect strong correlations between environmental variables and species richness, it is necessary to have strong patterns of species richness. While widespread species ranges overlap almost necessarily (Colwell *et al.*, 2004), ranges of range-restricted species are less likely to do so (Grenyer *et al.*, 2006; White & Kerr, 2006) and therefore range-restricted species richness may display little detectable variation along broad environmental gradients. Thus, weak correlations between range-restricted and widespread species richness may misrepresent underlying environmental determinants for those patterns. New models that can predict differences in species richness among range-restricted and widespread species assemblages would be helpful in determining if the observed weak correlations accurately represent differences in the way these assemblages respond to environmental gradients.

Spatially explicit models of species range spread (spreading-dye models; Jetz & Rahbek, 2001) have been used to investigate a variety of macroecological questions (Jetz & Rahbek, 2001; Colwell *et al.*, 2004; Kerr *et al.*, 2006; Storch *et al.*, 2006; Rahbek *et al.*, 2007; Currie & Kerr, 2008). Originally developed to test for mid-domain effects (Colwell & Lees, 2000; Jetz & Rahbek, 2001; but see Currie & Kerr, 2008), these models randomly seed a

landscape with species ranges, allowing them to expand in a probabilistic manner. Ranges are constrained only by hard domain boundaries and a pre-determined range size–frequency distribution. Recently, Storch *et al.* (2006) and Rahbek *et al.* (2007) expanded these types of models to incorporate environmental influences. By making the probability of range spread dependent on underlying environmental conditions, they showed that spatially explicit predictions could be generated based on any number of hypotheses. These models have the advantage of generating spatially explicit predictions of diversity gradients that integrate environmental and range size constraints.

A weak correlation between widespread and range-restricted species richness may arise for two reasons, independently or in combination. First, the correlation may be weak because different factors determine range-restricted and widespread species richness, respectively. Second, the weak correlation might arise in whole or in part because the small number of total occurrences and lower likelihood of range overlap among sampling quadrats for range-restricted species limits the formation of strong spatial patterns. We take a dual approach to evaluating these possibilities. The first uses spatially explicit range models (Storch *et al.*, 2006; Rahbek *et al.*, 2007) that incorporate constraints on overlap potential and occurrence numbers imposed by different range sizes. The second uses a novel sampling scheme that avoids the potentially confounding effects of low range overlap among range-restricted species that arise in traditional quadrat-based analyses.

We develop a series of models to determine if a weak correlation between widespread and range-restricted species richness is expected when the richness trends of these assemblages are determined by different environmental factors, as suggested by numerous authors (e.g. Jetz & Rahbek, 2002; Kreft *et al.*, 2006; Rahbek *et al.*, 2007). Our models, based on the approach of Storch *et al.* (2006) and Rahbek *et al.* (2007), predict the expected correlations between range-restricted and widespread species richness under a set of alternative hypotheses. These models predict the correlation between the two assemblages while explicitly including the effects of differing ranges sizes. Specifically we determine the predicted correlation when: (1) range-restricted species richness tracks widespread species richness; (2) temperature (the strongest single predictor of widespread species richness) determines both range-restricted and widespread species richness, respectively; (3) topographic heterogeneity (the strongest single predictor of range-restricted species richness) determines both range-restricted and widespread species richness; (4) topographic heterogeneity determines range-restricted species richness and temperature determines widespread species richness; and (5) the richness of the two assemblages are spatially random. The latter two hypotheses differ in that the former accounts for any correlation that may arise due to collinearity between climate and topography across broad geographical gradients.

Our second, complementary, approach to evaluating environmental determinants of widespread and range-restricted species richness uses a novel test that excludes constraints on pattern

detection for assemblages with small ranges that were inherent in previous analyses. Limited potential for range overlap among range-restricted species and a small number of total occurrences prevents range-restricted species richness from forming strong spatial gradients; alternatively, most environmental variables show strong spatial trends at broad scales. Since the strength of correlations detected in regressions from conventional grid systems is dependent on the variables showing similar spatial structuring (McPherson & Jetz, 2007), standard analyses may miss (or underestimate) key influences of spatially structured environmental variables on range-restricted species richness. Therefore, a method that is not dependent on the degree of spatial structuring of richness is required to assess the influence of environmental variables on range-restricted species richness. We achieved this by dividing the Americas into quantiles based on environmental variables and then assessing richness in these quantiles. By assessing richness in large divisions composed of environmentally consistent areas, rather than individual grid cells, our test can potentially detect environmental effects on range-restricted species richness that are masked by standard analyses.

Our dual approach to comparing environmental determinants of widespread and range-restricted species richness patterns allows for the comparison of findings using different methods that evaluate different predictions. Thus, consistency in the results from the two methods will render our conclusions more robust. Overall, our combined modelling and quantile-based analyses deconstruct the relationship between widespread and range-restricted species diversity and provide new insight into the environmental basis for species richness among widespread and range-restricted species assemblages.

## MATERIALS AND METHODS

### Range maps and species richness

The geographical ranges for terrestrial mammals of the western hemisphere were obtained from NatureServe (<http://www.natureserve.org/>) and converted into raster format. Mammals that are only found on islands were excluded from this analysis, leaving a total of 1677 species. Using ArcInfo GRID (ESRI, 2004), we calculated the range size of each species within continental North and South America and then placed the species in ascending order based on their range size. Following Jetz & Rahbek (2002), we considered the 419 species in the first quartile of range sizes to be range restricted and those in the fourth quartile (420 species) to be widespread.

To evaluate species richness, we divided the continental Americas into equal-area quadrats of 10,000 km<sup>2</sup>. After removing those quadrats with <50% land area, 3668 such quadrats remained. Species richness was calculated as the number of species ranges that overlapped a quadrat. The statistical significance of the correlation between widespread and range-restricted species richness was computed using Dutilleul's modified *t*-test to account for spatial autocorrelation.

### Environmental data

We downloaded annual mean temperature, annual temperature range, minimum temperature of the coldest month, annual precipitation, and elevation data at 30 arcsec resolution from WorldClim (<http://www.worldclim.org/>). MODIS annual net primary productivity (NPP) data at a 1-km resolution was obtained from the NASA Earth Observatory System ([https://lpdaac.usgs.gov/lpdaac/products/modis\\_products\\_table](https://lpdaac.usgs.gov/lpdaac/products/modis_products_table)). To obtain land-cover variety (a measure of habitat heterogeneity), we used the land-cover classification from Global Landcover 2000 (<http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php>), a dataset which includes 22 land-cover classes derived from 1-km resolution SPOT4 vegetation sensor data. These data layers were then projected onto our quadrat system and the mean (for climate data), range (for elevation) and number of classes (for land cover) for each 10,000-km<sup>2</sup> quadrat were extracted.

### Environmental predictors of species richness

To determine the strongest predictors of widespread and range-restricted species richness, we regressed widespread and range-restricted species richness on each of our environmental variables. We also tested models that included quadratic terms to account for potential nonlinearity. Our goal was not to identify the combined model that explained the maximum amount of variation in richness, but rather to isolate the environmental variables that are most strongly related to richness for our subsequent analyses. To determine if predictors remained significant after accounting for spatial autocorrelation (the non-independence of proximate data points), we also performed conditional autoregression (CAR) using the *spdep* package (Bivand *et al.*, 2007) for R, version 2.6.0 (R Development Core Team, 2007). For CARs, we defined the spatial weights matrix (**W**) in which the influence of location *i* on location *j* ( $w_{ij}$ ) declined with the distance ( $d_{ij}$ ) between them, with the decline taking the form  $w_{ij} = d_{ij}^{-\alpha}$ . For each regression, we examined three alternative values for  $\alpha$  (1.0, 1.5 and 2.0) and chose the one that resulted in the lowest level of spatial autocorrelation in model residuals. In all cases, distances greater than the maximum distance at which significant autocorrelation remained in ordinary least squares (OLS) residuals were given spatial weights of zero (Lichstein *et al.*, 2002). Pseudo-*R*<sup>2</sup> values were calculated following Lichstein *et al.* (2002).

### Simulation models

We used a basic spreading-dye model (Jetz & Rahbek, 2001; Kerr *et al.*, 2006) in which a species is placed at a random location on a map and its range is then allowed to grow randomly until a predetermined size is reached. The total richness and range size frequency distribution of the modelled assemblages were the same as the real world assemblages. Like Rahbek *et al.* (2007) and Storch *et al.* (2006), we altered quadrat probabilities of colonization to produce predictions based on alternative hypotheses. For each of our models, we performed 999 repetitions and

computed expected correlations between widespread and range-restricted species richness. The observed correlation was then compared to the distribution of Pearson's  $r$ -values from the simulations. It was not necessary to account for spatial autocorrelation using Dutilleul's (1993) method since  $P$ -values were determined directly from comparison with the expected distribution of Pearson's  $r$ -values and not  $t$ -tests.

To determine the expected pattern when range-restricted species richness tracks widespread richness, we made colonization probabilities for range-restricted species proportional to the widespread species richness of a quadrat, specifically

$$P_i = \frac{S_{wi}}{\sum S_w}$$

where  $S_{wi}$  is the number of widespread species in quadrat  $i$  and  $\sum S_w$  is the sum of widespread richness across all quadrats. To determine what correlation should be observed between widespread and range-restricted richness patterns if they both resulted from identical underlying processes, we compared the observed widespread richness values and modelled range-restricted values.

Next we determined the expected correlations when gradients of richness among widespread and range-restricted species were: (1) both determined by minimum temperature; (2) both determined by topographic heterogeneity (elevation range within a quadrat); (3) determined differently with widespread richness determined by minimum annual temperature and range-restricted richness by topographic heterogeneity. To accomplish this goal, we constructed two probability-of-colonization maps of the general form

$$P_i = \frac{E_i}{\sum E}$$

where  $E_i$  is the value of the environmental value in quadrat  $i$  and  $\sum E$  is the sum across all quadrats. To ensure comparability between maps based on environmental factors with different units, we first standardized the temperature and heterogeneity values so that both had means of 0 and standard deviations (SD) of 1. However, this resulted in negative values and thus negative probabilities. To eliminate this problem, we found the minimum value (MinV) across both sets and added  $\text{MinV} + 1$  to all standardized quadrat values. The distribution of predicted correlations was determined from the richness values of assemblages modelled on the relevant probability maps.

Our last hypothesis proposed that the richness of our two assemblages resulted from spatially random dynamics. To test this hypothesis, we made all colonization probabilities equal, simulated widespread and range-restricted assemblages and then computed the correlations between these simulated assemblages.

### Temperature and topographic heterogeneity divisions

To disentangle and identify common and assemblage-specific environmental constraints on widespread and range-restricted

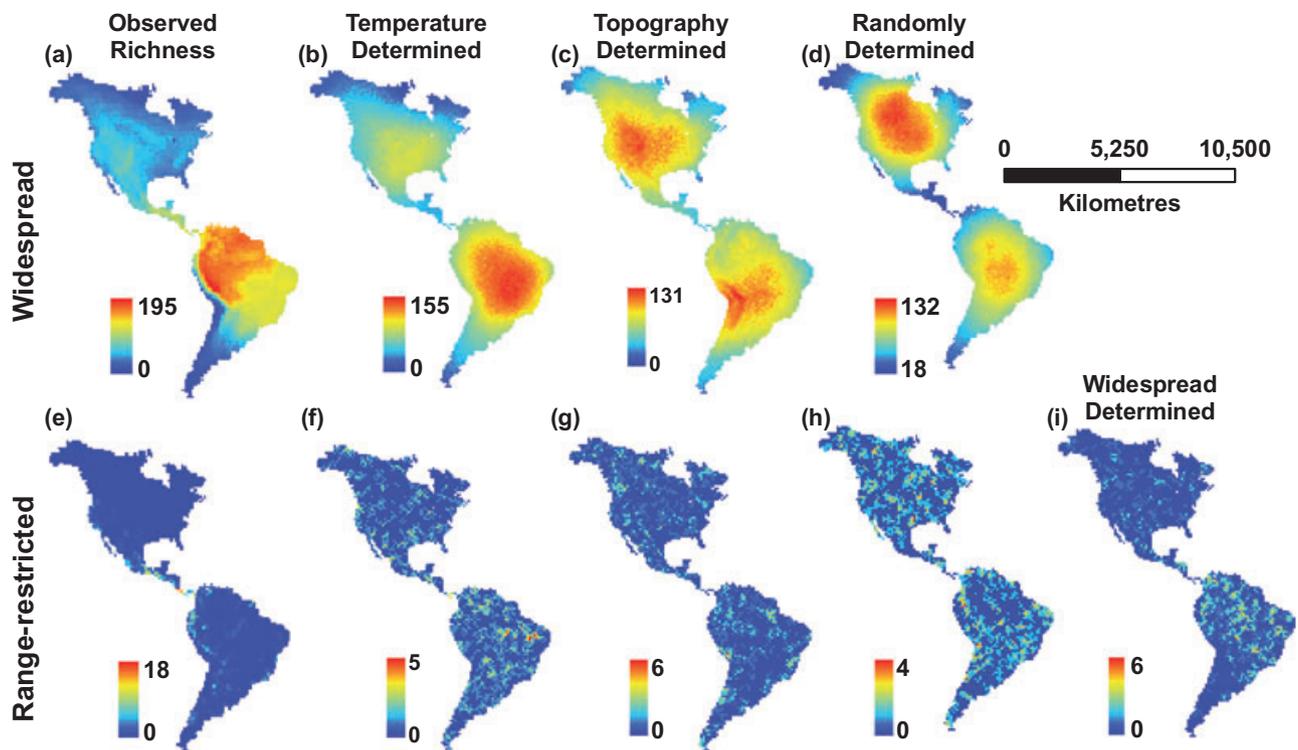
species richness, we devised a novel sampling scheme intended to avoid the limitation of low potential range overlap among range-restricted species. We generated divisions of similar temperature (or topographic heterogeneity) by ranking our quadrats from lowest to highest with respect to minimum annual temperature or topographic heterogeneity and then grouping quadrats into 5% quantiles (see Table S1 and Fig. S1 in Supporting Information). The mean quantile areas  $\pm 1$  SD were  $1,847,840 \pm 14,210$  km<sup>2</sup> for minimum annual temperature and  $1,847,444 \pm 18,303$  km<sup>2</sup> for topographic heterogeneity (there was some variation in the area of the divisions because 9 of the divisions contained one less quadrat than the remaining 11 divisions and not all quadrats contained 100% land area). The number of range-restricted and widespread species present in each quantile was then determined. Finally, we calculated the correlations between the richness of range-restricted and widespread species across these quantiles. Pearson's  $r$ -values were not adjusted for spatial autocorrelation since quadrats within quantiles were not always spatially contiguous and were often more spatially disparate than quadrats in different quantiles, rendering spatial weights or connectivity matrices nonsensical.

To ensure that our results were not a result of using 5% quantiles to compare richnesses, we performed three additional procedures. First, we evaluated whether richness was related to the range of temperatures (or heterogeneity values) within a division, or to the mean geographical distance between quadrats. When statistically significant correlations between richness and distance or temperature (heterogeneity) range were present, we used path analysis to determine whether these correlations accounted for the observed relations between widespread and range-restricted species richness. We also evaluated correlations between widespread and range-restricted division richnesses by randomly assigning quadrats to a division and recalculating species richness for both assemblages. We repeated this process 999 times and compared our observed correlations to the random expectation. Lastly, we divided the Americas into 30, rather than 20, divisions and recalculated the correlations between widespread and range-restricted richness.

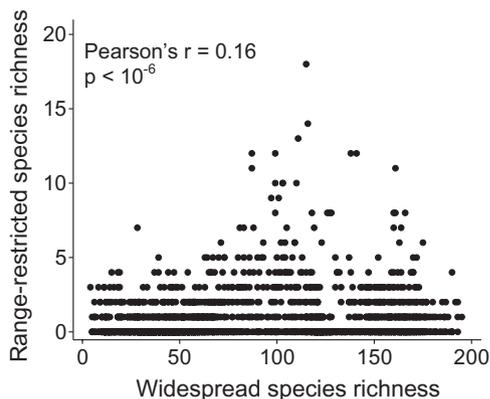
## RESULTS

Species richness showed an obvious geographical gradient for widespread species, but not for range-restricted species (Fig. 1a, d). Range-restricted and widespread species richness were only weakly correlated across the combined mainland area of North and South America (Fig. 2;  $r = 0.16$ ,  $P < 0.01$ , d.f. = 264.3 using Dutilleul's (1993) modified  $t$ -test to correct for spatial autocorrelation).

Minimum annual temperature predicted widespread species richness better than any other variable (quadratic OLS  $R^2 = 0.78$ ; Table S2). Mean annual temperature, annual temperature range, annual precipitation and annual NPP also relate strongly to the richness of widespread species (OLS  $R^2 = 0.49$ – $0.74$ ; Table S2). However, indices of habitat heterogeneity, including land-cover variety and topographic heterogeneity (elevation range within a quadrat), predicted richness of widespread species very poorly.



**Figure 1** Observed and modelled patterns of widespread (a–d) and range-restricted (e–i) mammal species richness in the Americas. Shown are the actual patterns of richness (a, e) and representative patterns from model runs. Parts (b) and (f) depict the pattern when widespread and range-restricted richness are determined by minimum temperature and parts (c) and (g) that determined by topographic heterogeneity. Parts (d) and (h) show the patterns when range placement and spread is spatially and uniformly random and (i) shows the predicted range-restricted pattern when range spread tracks widespread species richness. Maps use a Lambert azimuthal projection.



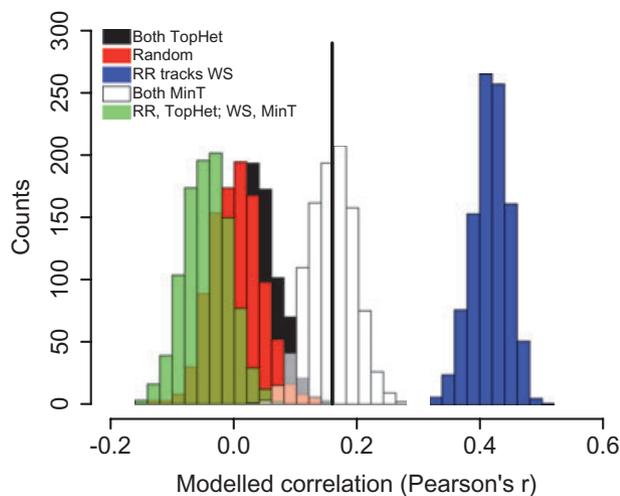
**Figure 2** Relationship between range-restricted and widespread species richness in 10,000-km<sup>2</sup> quadrats ( $n = 3668$  quadrats) in the continental Americas.

For range-restricted species, topographic heterogeneity predicted richness better than any other variable we measured but rather weakly (quadratic OLS  $R^2 = 0.15$ ; Table S2), accounting for far less variation in range-restricted species richness than aspects of climate do for richness of widespread species. These results are similar for both OLS and conditional autoregressive models (Table S2). Also, after fitting CARs, spatial autocorrela-

tion of residuals was greatly reduced in all models (Moran's  $I$  of OLS residuals ranged from 0.15–0.90; Moran's  $I$  of CAR residuals ranged from 0.02–0.28), though still statistically significant ( $P$ -values  $\ll 10^{-5}$ ). Moran's  $I$ -values of the residuals from the best predictive models for widespread (minimum temperature) and range-restricted (topographic heterogeneity) species were 0.13 and 0.03, respectively.

Our null model analysis (Fig. 1b–d, f–i) showed that when range-restricted species richness is constrained to track widespread species richness, the expected correlation between the richness of widespread and range-restricted species is only 0.42 (Fig. 3). The actual correlation between the two patterns was 0.16, a value that is lower than any of the simulated correlations ( $P = 0.001$ ). However, the mean expected correlation when both patterns are determined by temperature was almost identical to the observed correlation ( $r = 0.16$ ,  $P = 0.49$ ). Alternately, when both patterns are determined by topographic heterogeneity, the expected correlation is lower than the actual correlation ( $r = 0.027$ ,  $P = 0.001$ ). This is also the case when both patterns are determined randomly ( $r = 0.004$ ,  $P = 0.001$ ) or when topographic heterogeneity determines range-restricted species richness and temperature determines widespread species richness ( $r = -0.04$ ,  $P = 0.001$ ).

Using our quantile-based sampling method, we found that widespread and range-restricted species have qualitatively



**Figure 3** The observed correlation between widespread and range-restricted species richness and the expected correlation based on alternative hypotheses. The observed correlation is represented by the vertical line. Each histogram represents the correlation between widespread and range-restricted species richness for 999 simulations. The black histogram is the prediction when range-restricted and widespread species richness are both determined by topographic heterogeneity (TopHet), red is the prediction from statistically independent processes, blue is the prediction when range-restricted richness (RR) tracks widespread richness (WS), white is the prediction when both are determined by minimum temperature (MinT) and green is the predicted correlation when widespread richness is determined by minimum temperature and range-restricted richness by topographic heterogeneity.

similar distributions of species richness across minimum temperature quantiles: both were unimodal with richness peaks in a warm, but not the warmest, quantile (13th quantile for widespread species, 14th for range-restricted species; Fig. 4a, c). By contrast, the richness patterns for topographic heterogeneity quantiles are dissimilar: while widespread species richness is quite consistent across divisions, range-restricted species richness increases rapidly toward areas including the highest elevations (Fig. 4b, d).

More importantly (and quantitatively), richness of both assemblages is highly correlated for minimum temperature quantiles ( $r = 0.81$ ,  $P < 10^{-5}$ , Fig. 4e), but not for topographic heterogeneity quantiles ( $r = -0.22$ ,  $P > 0.30$ , Fig. 4f). Although the relationship across minimum temperature quantiles does not appear to be strictly linear, as expected if temperature affected both groups identically, the high correlation between richness of the assemblages strongly suggests shared responses to minimum temperature. This result does not arise as a by-product of quantile-based sampling. When quadrats were randomly assigned to divisions and both widespread and range-restricted species were tallied within them, the expected correlation between range-restricted and widespread species richness across divisions ( $r = 0.15$ ) was far lower than the observed correlation between temperature quantiles ( $P = 0.001$ , based on 999

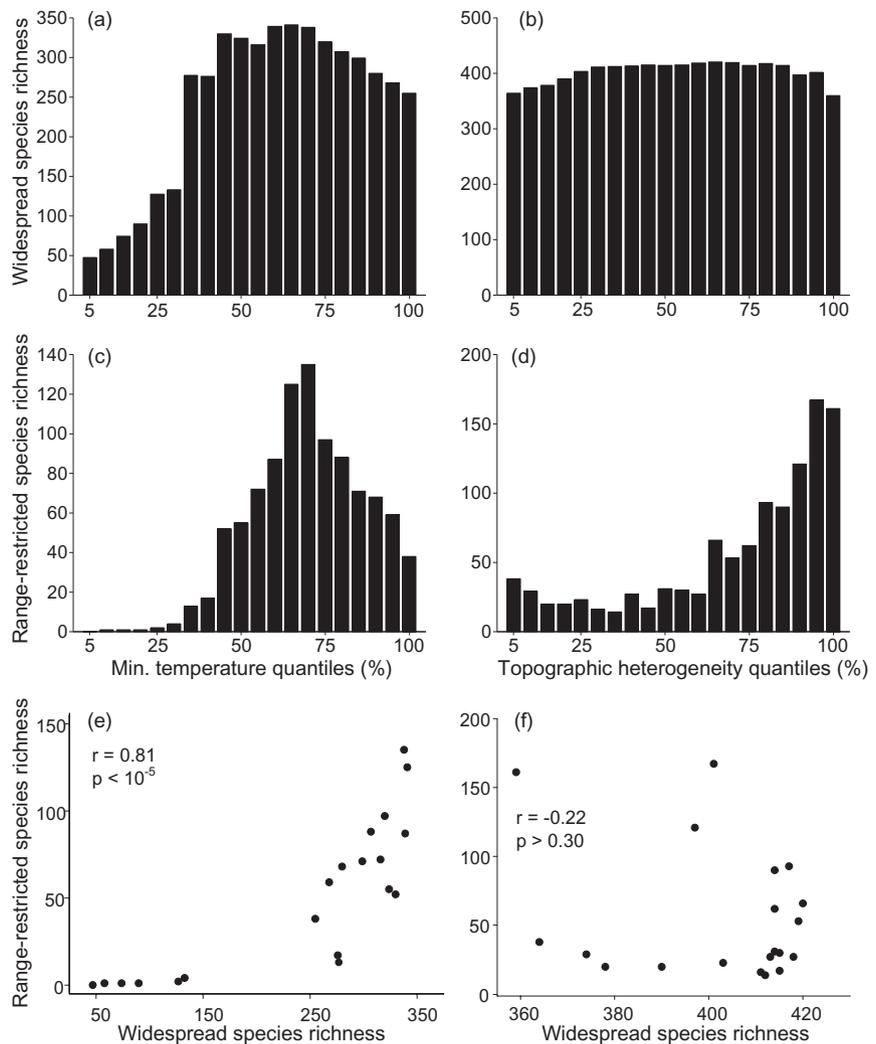
null model repetitions). Nor were our results a product of having chosen to divide the Americas into 20 equal-area zones, as dividing quadrats into 30 divisions, rather than 20, did not change our results (Fig. S2). Furthermore, the significant correlation between widespread and range-restricted species richness across temperature divisions does not reflect systematic variation in temperature or heterogeneity ranges or spatial relationships (mean distance) within divisions (Appendix S1, Fig. S3). Collectively, our results indicate that species richness of range-restricted and widespread species are differentially affected by topographic heterogeneity, but that they share common responses to climate, specifically minimum temperature.

## DISCUSSION

Jetz & Rahbek (2002) demonstrated that there are distinct differences between geographical patterns of widespread and range-restricted species. The subsequent conclusion that the diversities of these two species assemblages are driven by separate environmental components relies on the assumption that apparently disparate geographical patterns indicate differential environmental control. This assumption is bolstered by the observation that widespread species richness varies strongly with climate but range-restricted richness is correlated with topographic variability instead (Jetz & Rahbek, 2002; Kreft *et al.*, 2006; Rahbek *et al.*, 2007). However, as some authors have speculated (Grenyer *et al.*, 2006; White & Kerr, 2006), these differences could appear, at least in part, because of sampling effects arising from the potential for overlap of small or large ranges in gridded, bounded domains.

To account for these sampling effects, we created a series of null models that predicted the degree of correlation between these two assemblages when their richnesses were determined identically, randomly or differentially by temperature (widespread species) and topography (range-restricted species). These models revealed that strong correlations are unlikely even when richnesses are identically determined, demonstrating the limitation of standard environment–richness regressions for comparing widespread and range-restricted species richness and emphasizing the need to develop novel approaches for examining these relationships.

The expected correlation when richnesses of both assemblages are determined by temperature was nearly identical to the observed correlation. This is consistent with the hypothesis that temperature influences the richness patterns of both widespread and range-restricted species. More importantly, models based on spatially random patterns, common influence of topographic heterogeneity or differential environmental control, all failed to accurately predict the observed correlation between widespread and range-restricted richness. Thus, these can be rejected as sole explanations of the weak, but non-zero, correlation between widespread and range-restricted species richness. However, while our modelling results are consistent with the hypothesis that temperature determines both richness patterns, our models also indicate that range-restricted richness does not simply track widespread species richness. Indeed, it is unlikely that both



**Figure 4** Widespread and range-restricted species richness in 20 equal-area divisions based on minimum annual temperature (a, c, e) and topographic heterogeneity (measured as elevation range; b, d, f): (a) and (b) are for widespread species, (c) and (d) are for range-restricted species and (e) and (f) show the correlation between widespread and range-restricted species richness based on minimum annual temperature and topographic heterogeneity, respectively.

widespread and range-restricted species richness are determined solely by temperature given that topographic heterogeneity, not temperature, is the strongest (but still weak) univariate predictor of range-restricted species richness.

The quantile-based technique we developed to analyse richness gradients clarifies the influence of temperature and topographic heterogeneity on widespread and range-restricted species richness. Numerous previous studies, like ours, have found that the richness of these assemblages is only weakly correlated across space (e.g. Jetz & Rahbek, 2002; Lennon *et al.*, 2004; Orme *et al.*, 2005; Grenyer *et al.*, 2006, and many others) and have attributed these disparate patterns to different determinants of richness. However, other authors have speculated that these correlations may be low, at least in part because small species ranges are unlikely to overlap and thus are unable to form strong spatial gradients (Grenyer *et al.*, 2006; White & Kerr, 2006). Our approach avoids this limitation by sampling richness in environmentally consistent, but not necessarily spatially continuous, areas. Our findings demonstrate that similar trends in richness of widespread and range-restricted species exist across minimum annual temperature quantiles in the Americas. This

analysis reveals a common, assemblage-independent, relationship between temperature and species richness. Conversely, assemblage-specific topographic effects were evident in the divergent patterns for range-restricted and widespread species in topographic heterogeneity quantiles. Widespread species showed little response to topographic heterogeneity, while range-restricted species exhibited an obvious pattern that is reminiscent of that observed for global avian species richness (Davies *et al.*, 2007). These findings do not depend on the two patterns showing similar degrees of spatial structuring, which is known to be required to generate strong statistical relationships based on conventional two-dimensional grid systems (McPherson & Jetz, 2007) that lie at the heart of nearly all macroecological research into spatial variation in species richness.

A key question arising from our findings is what are the relative importances of common temperature- and assemblage-specific topographic heterogeneity effects on determining patterns of species richness for widespread and range-restricted species. Clearly, temperature is of greater importance for widespread species as it predicts a substantial amount of the variation in species richness (e.g. Jetz & Rahbek, 2002; Evans *et al.*,

2005; this study). However, the question of whether temperature or topographic heterogeneity is of greater importance for range-restricted species is less straightforward. Our regression analysis suggests that topographic heterogeneity may be more important, though such inferences may be limited by the sampling constraints associated with small ranges. Alternatively, our modelling results showed that assemblage-specific effects of topographic heterogeneity need not be invoked to predict the correlation between widespread and range-restricted species richness. Future work should focus on evaluating the relative importance of assemblage-specific responses to topographic heterogeneity and assemblage-independent responses to temperature as determinants of range-restricted species richness.

Our analysis demonstrates that species richness gradients can be dissimilar but still result from similar underlying environmental determinants. It is likely that the same mechanisms associated with temperature shape species richness patterns for both range-restricted and widespread species. In contrast, mechanisms associated with the effects of topographic heterogeneity, such as increased habitat complexity (Kerr & Packer, 1997; Kerr *et al.*, 2001; Rahbek & Graves, 2001) and vicariant diversification triggered by mountain uplift (Hughes & Eastwood, 2006; Thomas *et al.*, 2008), likely influence patterns of range-restricted species richness more strongly. This may be related to a tendency for range-restricted species to have narrower niches than widespread species (Brown *et al.*, 1996; Thompson *et al.*, 1999): increased habitat complexity associated with montane environments would thus increase the number of range-restricted species that are able to coexist within a small area but not affect the numbers of widespread species. In addition, diversification triggered by mountain uplift may be more important for patterns of range-restricted species richness because of poorer dispersal abilities among range-restricted species (Brown *et al.*, 1996; Böhning-Gaese *et al.*, 2006). This limited dispersal ability may result in greater isolation and allopatric speciation among range-restricted species and thus disproportionate increases in range-restricted species richness, since range size tends to be at least somewhat similar among closely related species (Jablonski, 1987; Mouillot & Gaston, 2007; Waldron, 2007). Distinguishing among such mechanisms represents an important area for further work. The identification of common and assemblage-specific responses to particular environmental determinants is a valuable, perhaps essential, prerequisite for developing improved tests of these proposed mechanisms.

Our finding that, despite the apparent dissimilarity between widespread and range-restricted species richness gradients, temperature actually affects both patterns in a similar way, highlights the need for macroecological studies to go beyond the evaluation of spatial pattern (Kerr *et al.*, 2007). The expanded use of models to evaluate the validity of predictions and to generate new ones, combined with novel empirical techniques and increasingly available datasets, will lead to stronger tests of macroecological theories. Such tests are essential in directing broad-scale approaches for responding to the globally pervasive effects of climate and land-use changes (Foley *et al.*, 2005; Malcolm *et al.*, 2006) on biodiversity and ecosystem services.

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## SUPPORTING INFORMATION

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

**Figure S1** Maps of 5% quantiles based on minimum temperature or topographic heterogeneity.

**Figure S2** Widespread and range-restricted species richness in 30 divisions based on minimum temperature or topographic heterogeneity.

**Figure S3** Path diagrams incorporating effects of variable range and spatial position of quadrats within quantiles.

**Table S1** Bounds of 5% quantiles based on minimum temperature or topographic heterogeneity.

**Table S2**  $R^2$  and Akaike information criterion (AIC) values of richness–environment regressions.

**Appendix S1** Path analysis results.

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