RESEARCH PAPER

WILEY | **Global Ecology and Biogeography** | A Journal of Macroecology

The origins and maintenance of global species endemism

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Abstract

Aim: We test macroecological hypotheses (*H1: long-term climate stability; H2: climate seasonality; H3: climate distinctiveness or rarity; and, H4: spatial heterogeneity in contemporary climate, topography or habitat*) proposed to explain broad-scale patterns of total species endemism.

Location: Continental areas worldwide and zoogeographical realms.

Methods: Using species distribution maps for mammals and amphibians, we calculated five metrics of species endemism, based on inverse and median range size, and range size cut-offs. We performed multi-model averaging. We tested the accuracy of fitted models using cross-validation, comparing observed versus predicted values of endemism among zoogeographical realms.

Results: Model averaging showed that species endemism for amphibians and mammals was statistically related to all set of predictors (*H1*, *H2*, *H4* and richness), except for climate distinctiveness (*H3*). Effect sizes for spatial heterogeneity were larger and more consistent among zoogeographical realms than the effect sizes of climate stability. The effect of species richness on species endemism varies widely and depends on the metric of endemism and taxonomic group used in the analysis. Cross-validation across all zoogeographical realms showed that predictions of endemism systematically fail for both taxa. In most cases, low to moderate endemism is predicted reasonably well. However, areas with high numbers of endemic species are systematically under-predicted.

Main conclusions: Our results are not consistent with any of the processes hypothesized to create and maintain global patterns of endemism. Although we found statistically significant relationships, they failed the stronger test of a causal relationship: accurate prediction in independent data. The inconsistent effect of richness in our models suggests that patterns of endemism are not driven by the same variables as total richness. Patterns of endemism have no consistent relationships with climatic stability among zoogeographical realms, so suggestions that endemism reflect climatic stability are likely due to collinearity with other factors, especially spatial heterogeneity.

KEYWORDS
amphibians, climate seasonality, climate stability, climate velocity, endemic species, endemism, macroecology, mammals, spatial heterogeneity, species richness

1 | INTRODUCTION

Exceptional numbers of species with relatively small ranges are concentrated in some regions of the Earth (Jetz & Rahbek, 2002), creating broad-scale patterns of species endemism (Lamoreux et al., 2006). Although several factors have been proposed to explain these patterns, including climate, spatial heterogeneity, historical factors and biotic interactions (Fjeldså & Lovett, 1997; Jansson, 2003; Ohlemüller et al., 2008; Sandel et al., 2011), their relative roles are still contentious.

One prominent hypothesis invoking the effect of historical climate on species endemism (*H1: long-term climate stability hypothesis*; Dynesius & Jansson, 2000; Jansson & Dynesius, 2002) suggests that recurrent and rapid climatic shifts, caused by periodic changes in the orbit of the Earth during the Quaternary [i.e., Milankovitch oscillations over 10–100 thousand year periods; Berger (1988)], led to significant changes in the size and the location of the geographical distributions of clades. Orbitally forced species range dynamics may contribute to present-day gradients of endemism in three ways (Dynesius & Jansson, 2000). First, areas of high climatic instability may select for species with high dispersal abilities that enable them to track rapid spatial displacement of climatic conditions, resulting in species with broader distributions. Second, climatic instability may reduce the likelihood of specialization on a narrow array of climatic conditions, which could reduce speciation rates and limit the evolution of novel clades. Third, areas with unstable climates may have higher extinction rates, with small-ranged species facing greater extinction risks because of the challenges of surviving stronger climatic variability. In contrast, areas of high climatic stability select for species with low dispersal capabilities, offering opportunities for persistence and further diversification. Sandel et al. (2011) show that species with broad geographical ranges are associated with areas of high climate-change velocity (a variable that measures climate stability) during the Last Glacial Maximum (LGM—21,000 years ago). They further argue that species with small range sizes and low dispersal capabilities have gone extinct in areas with high climate velocity, most likely because they were unable to cope with strong climate displacement prevalent in these areas (Sandel et al., 2011). Fjeldså and Lovett (1997) offer another perspective: environmentally stable areas may have enabled survival and concentration of young species with small ranges, and also of relictual taxa with narrow ranges. Fjeldså and Lovett (1997) note, however, that extinction in climatically unstable areas is not essential to explain macroecological patterns in this model of endemism.

A second set of hypotheses proposes that contemporary climate shapes the spatial distribution of endemism. First, greater seasonal variation in temperature may select for species that can tolerate a wider temperature range (Sunday, Bates, & Dulvy, 2011), resulting in species with wider climatic niches, and therefore larger geographical ranges. In contrast, low seasonality may select for species with narrower thermal tolerances, resulting in species with smaller geographical ranges (*H2: climate seasonality hypothesis*; Addo-Bediako,

Chown, & Gaston, 2000). Second, areas that are climatically distinct from their regional surroundings may select for species adapted to these conditions, which in turn may promote small range sizes in those localities (*H3: climate distinctiveness or rarity*; Ohlemüller et al., 2008).

Another hypothesis proposes that spatial heterogeneity (*H4: spatial heterogeneity in contemporary climate, topography or habitat*) is the main factor that creates and maintains patterns of species endemism. Spatial heterogeneity creates more ecological niche opportunities and resource partitioning in a given region (Chesson, 2000), and it promotes the persistence, adaptation and diversification of range-restricted species (Jetz & Rahbek, 2002; Ohlemüller et al., 2008).

In sum, several environmental drivers (climate – whether past or current –and/or spatial heterogeneity) could shape spatial variation in the richness of range-restricted species. If one or more of these are the drivers of global variation in endemic richness, they must not only statistically explain substantial variance in gradients of endemic species richness (Møller & Jennions, 2002), but those correlations must also predict patterns of endemism in datasets that were not used in building the original model (e.g., predict trends successfully in independent geographical areas). This is important because the core purpose of this work is to identify meaningful potential determinants of endemism and the extent to which these determinants are consistent across regions (Wenger & Olden, 2012). A model's greatest test is in whether it is rigorously validated (Wenger & Olden, 2012). Notwithstanding that the hypotheses mentioned above have received some support, tests of those models against independent data have not yet been undertaken. If the hypothesized factors drive global variation in endemic richness, then consistent relationships between predictor variables and endemic richness should be observed (Møller & Jennions, 2002) and models should predict the response variable (Rykiel, 1996).

Here, we test each of these hypotheses by examining to what extent broad-scale patterns of endemism relate to the aspects of temporal and spatial climatic stability and heterogeneity using different metrics of endemism. We evaluate the robustness of the statistical models using cross-validation among zoogeographical realms. We ask whether the strength of the signal is strong enough to yield informative predictions of numbers of endemic species in independent geographical areas, that is, whether the predictions are unbiased.

2 | MATERIAL AND METHODS

2.1 | Species distributions

We used worldwide species distribution maps (IUCN, 2014) for terrestrial mammals (*n* = 5,291) and amphibians (*n* = 6,312) and projected them onto the World-Behrmann projection to preserve area across the extent of the analysis.

2.2 | Spatial resolution

To test for the effect of spatial resolution, we used various spatial resolutions. First, we overlaid vector maps of species distributions onto grids of approximately 1 degree (*c*. 110 km × 110 km, including all 10,445 grid cells as sampling units), the finest spatial resolution that is appropriate for this broad-scale analysis (Buckley & Jetz, 2008; Hurlbert & Jetz, 2007). Given the likelihood of scale dependence in patterns of species endemism (Belmaker & Jetz, 2011), and given that other studies have reported results at coarser spatial resolutions (Sandel et al., 2011), we evaluated the effect of three additional spatial resolutions (*c*. 200 × 200 km, 500 × 500 km and 1,000 × 1,000 km) on predictors' collinearity and strength of their relationships with species endemism. We included only grid cells consisting of more than 50% land area.

2.3 | Measuring species endemism

We constructed five metrics of endemism for each amphibian and mammal assemblage in a quadrat. Our operational definition of endemism is: the number of species with small geographical range size. For the first three metrics, we ordered species by range size, from smallest to largest, and we retained species when their range sizes fell within one of three cut-offs. First, we counted species as endemic if their ranges fell within the smallest quartile (25%) of the taxon's range size (Jetz & Rahbek, 2002). The second cut-off was an arbitrary, but commonly selected, range size of 50,000 km^2 (e.g., BirdLife International), which includes 71% of amphibians ($n_{\text{small-ranged}}$ = 4,527) and 34% of mammals ($n_{\text{small-ranged}}$ = 1,815). The third threshold was 250,000 km^2, which includes 85% of amphibians ($n_{\text{small-ranged}}$ = 5,354) and 54% of mammals ($n_{\text{small-ranged}}$ = 2,854). We used these definitions of endemism to compare differences among regions in the endemism–climate relationship (Sandel et al., 2011). For these three measures of endemism, we overlaid the species' ranges that satisfied each of these criteria, and we summed up the number of endemic species of mammals and amphibians in each grid cell. For the fourth metric of endemism, we wished to avoid defining arbitrary range size cut-offs (as described above), so we calculated species endemism by counting all species within each grid cell, but we weighted the count by the inverse of each species' range size (hereafter, WE or weighted endemism) (Crisp, Laffan, Linder, & Monro, 2001). The final metric is based on median range size (hereafter Median) of all species occurring in a grid cell. Because range size distributions are positively skewed, median range size is recommended instead of mean range size (Orme et al., 2006).

2.4 | Spatial taxonomic congruence of patterns of endemism

To measure the spatial taxonomic congruence of patterns of endemism, we compared the geographical variation of endemism for mammals and amphibians (i.e., taxonomic congruence; Lamoreux et al., 2006). For metrics based on range size cut-offs (first quartile, 50,000, 250,000 km^2), we compared the proportions of endemics in each of the four quartiles of range size (smallest quartile, etc.) between the two taxonomic groups. For WE and Median, we calculated the difference between amphibian and mammal endemism values.

2.5 | Climate and geographical predictors

To test the role of past and present climatic conditions on endemism, we used a set of variables from various sources. We used mean annual temperature (MAT), temperature seasonality (TS), total annual precipitation (PT) and precipitation seasonality (PS, the distribution of precipitation throughout the year), taken from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at 2.5 arc-minute resolution. We also used mean annual temperature during the Last Glacial Maximum (LGM, from the Community Climate System Model: CCSM4), and altitude, taken from WorldClim (Hijmans et al., 2005). Potential evapotranspiration (PET) at 30 arc-second resolution was obtained from Trabuco and Zommer (2009) and the global dataset of yearly actual evapotranspiration (AET, 5 arc-minutes) was downloaded from the Food and Agriculture Organization of the United Nations (https://www.fao.org/geonetwork). We projected all grids to the World-Behrmann equal area projection.

To measure long-term climate stability (*H1*), we used climate velocity (CV) as a metric that represents the displacement of climate in units of distance (metres) per time (years) (Loarie et al., 2009). CV is the ratio between the temporal and spatial components of MAT. The temporal component is the absolute difference between current MAT and MAT at the LGM (MAT_LGM (in °C/year) in a cell. The spatial component is the change of MAT relative to distance, that is, the change of MAT from grid cell to grid cell (in °C/m). We derived the spatial component from the calculated slope using the 'slope' function in ArcGIS 10.3 (ESRI, 2014). We adjusted areas with slopes equal to zero to small values (0.00001) to circumvent the issue of dividing by zero (Sandel et al., 2011).

To measure climate seasonality (*H2*), we used two proxies: temperature and precipitation seasonality (MATS and PS, respectively). To measure climate distinctiveness (*H3*), or rarity, we searched for similar climates within a moving window for each climatic measurement using four thresholds for each climatic metric (Ohlemüller et al., 2008). These were (1) MAT: ±0.5°C, ±1°C, ±2°C and ±4°C; (2) PT: ±10, ±100, ±200, ±500 mm; (3) PS: ±5, ±10, ±20 and ±50 mm; (4) TS: ±10, ±100, ±500, ±1,000 mm. For each metric and threshold, we added up the number of cells with climates outside these ranges, and we standardized this sum by the total number of cells in that window. For example, a grid cell surrounded by areas with distinctive climatic conditions (CD) has a regionally rare climate (CD values approaching 1). In contrast, CD values approaching 0 indicate climates similar to surrounding areas. We also tested for effects of different moving windows (5, 11 and 15 cells for each resolution). We excluded islands because they were sensitive to this moving window. For instance, a measurement of CD for a grid cell on a Caribbean island, based on a large moving window, is affected by continental cell values (which

clearly are not connected with the island in question). Therefore, we included only mainland areas for each continent.

To measure spatial heterogeneity (*H4*), we calculated and compared four metrics that account for most of the spatial heterogeneity (SH) in climate (AET, PET and MAT) and topography (we used altitude -ALT-, using elevation data from WorldClim). Variability of climate and topography within each grid cell was measured using three measurements: range, standard deviation and coefficient of variation.

Finally, we included species richness (hereafter Richness) as a covariate in analyses because, all other things being equal, the number of endemic species increases with species numbers generally (Crisp et al., 2001; Kerr, 1997). We aimed to evaluate potential mechanisms affecting numbers of endemic species independently of this covariate.

2.6 | Statistical analysis

2.6.1 | Endemism–climate relationship: first approximation

To explain the extent to which patterns of endemism relate to each predictor, we first explored nonparametric correlation coefficients between all metrics of endemism and each predictor. We used Spearman's rank correlation coefficients (r_s) to describe monotonic, often nonlinear, relationships.

2.6.2 | Model selection

We used multi-model averaging (Johnson & Omland, 2004) to evaluate the statistical support of explanatory variables in predicting broad-scale patterns of total species endemism. There are many candidate models that could plausibly account for present-day gradients of endemic species richness. Model averaging reduces model selection biases and accounts for model selection uncertainty (Grueber, Nakagawa, Laws, & Jamieson, 2011), so parameter estimates and predictions are, in that sense, relatively robust (Johnson & Omland, 2004). Model averaging simultaneously evaluates all hypotheses and identifies the best set of models based on stringent change in Akaike's Information Criterion (ΔAIC), providing a clear measure of the relative strength of evidence for tested hypotheses. Model averaging can also address issues related to collinearities among predictors (Peters et al., 2016).

We first transformed the dependent variable to improve homoscedasticity and normality, and the independent variables to improve linearity and the distributions of the underlying data (WE and Median endemism were the only metrics that allowed transformation, see Results). We then used conventional ordinary least squares (OLS) models. We z-standardized predictors associated with each causal hypothesis to compare the relative influence of each predictor on species endemism, obtaining standardized coefficient estimates, 95% confidence intervals and relative influence weights for each predictor. For model averaging, we set a stringent ΔAIC < 2 cut-off (Grueber et al., 2011). We tested how stable the conclusions were after controlling for spatial autocorrelation using simultaneous autoregressive (SAR) (Kissling & Carl, 2008).

Then, we evaluated the contribution of each variable using variation partitioning (Legendre & Legendre, 2012), and we constructed path analyses to test hypothesized causal relationships among those variables that are correlated with endemism. To compare and contextualize our path analysis results we used the well-documented statistical relationship between AET and richness (Currie, 1991; Hawkins et al., 2003), without implying a causal relationship.

2.6.3 | Cross-validation: estimating accuracy of models

To evaluate the capability of the models described above with independent data, we employed cross-validation across zoogeographical zones (Wenger & Olden, 2012). Validation with independent data is a way to measure the robustness of model predictability. For instance, Francis and Currie (2003) show that total species richness in any terrestrial biome can be predicted from the richness–climate relationship trained on data from all other areas of the world. We split the data into training and test samples. We used the training sample to build the model, and the test sample to evaluate whether the model successfully predicts species endemism in the held-out portion (Francis & Currie, 2003; Olden & Jackson, 2000). Here, we used zoogeographical realms (ZRs) from Holt et al. (2013) to split the dataset because they reflect potential region-specific patterns of diversification among vertebrate taxa. Spatial variation in diversification, or other historical processes, among ZRs might contribute to differences among them in terms of numbers of endemic species (Ricklefs, 2004). We constructed models using data from all ZRs but one. We then used each of these models to predict endemism in the ZR that had been held out. To evaluate the efficacy of cross-validation, we used root-mean-square error (RMSE), which measures prediction accuracy, with the advantage that this approach uses the same units as the response variable. Smaller RMSE values were associated with models with better correspondence between predicted and observed gradients of endemic species richness within a zoogeographical realm.

2.6.4 | Zero-inflation adjustments

Metrics of endemism based on range size cut-offs tend to contain a large proportion of zero values, associated with the absence of species with small geographical ranges. Here, we considered zero values to be 'true zeroes' because we are using species' ranges resolved at the finest spatial resolution at which it is reasonable to ascertain species' presence/absence (Buckley & Jetz, 2008). This zero-inflation phenomenon is important for statistical inferences here because zero-inflated datasets do not fit standard distributions (Martin et al., 2005). One way to correct this is by transforming total species endemism. Alternatively, zero-inflated (ZI) models have been developed to cope with the zero-inflation issue, modelling both the positive (non-zeroes) distribution and the excess of zeroes. A third approach, hurdle models, assumes that zeroes originate from a single process (structural zeroes), while ZI models assume that zero observations have two different origins (structural

and sampling zeroes) (Martin et al., 2005). We assume that the absence of endemic species in a grid cell results from one or more mechanisms tested here. For instance, Sandel et al. (2011) argue that endemic species were wiped out from areas of high CV, generating regions with structural zeroes that result from the process intrinsic to their hypothesis. So, we expect that hurdle models will be favoured over ZI models. We compared hurdle and ZI models using AIC values. We applied the cross-validation approach described above to evaluate the efficacy of hurdle models in predicting independent datasets.

All statistical analyses were performed in R v. 3.2.1 (R Core Team, 2017).

3 | RESULTS

3.1 | Spatial distribution of broad-scale patterns of endemism

As reported in previous studies (Jetz, Rahbek, & Colwell, 2004; Lamoreux et al., 2006) range-restricted amphibian and mammal species are concentrated in tropical and subtropical regions (Figure 1a and Supporting Information Figures S1 and S2). However, geographical congruence of mammal and amphibian endemism is not the general rule, and it depends upon the metric used to measure endemism (Figure 1b and Supporting
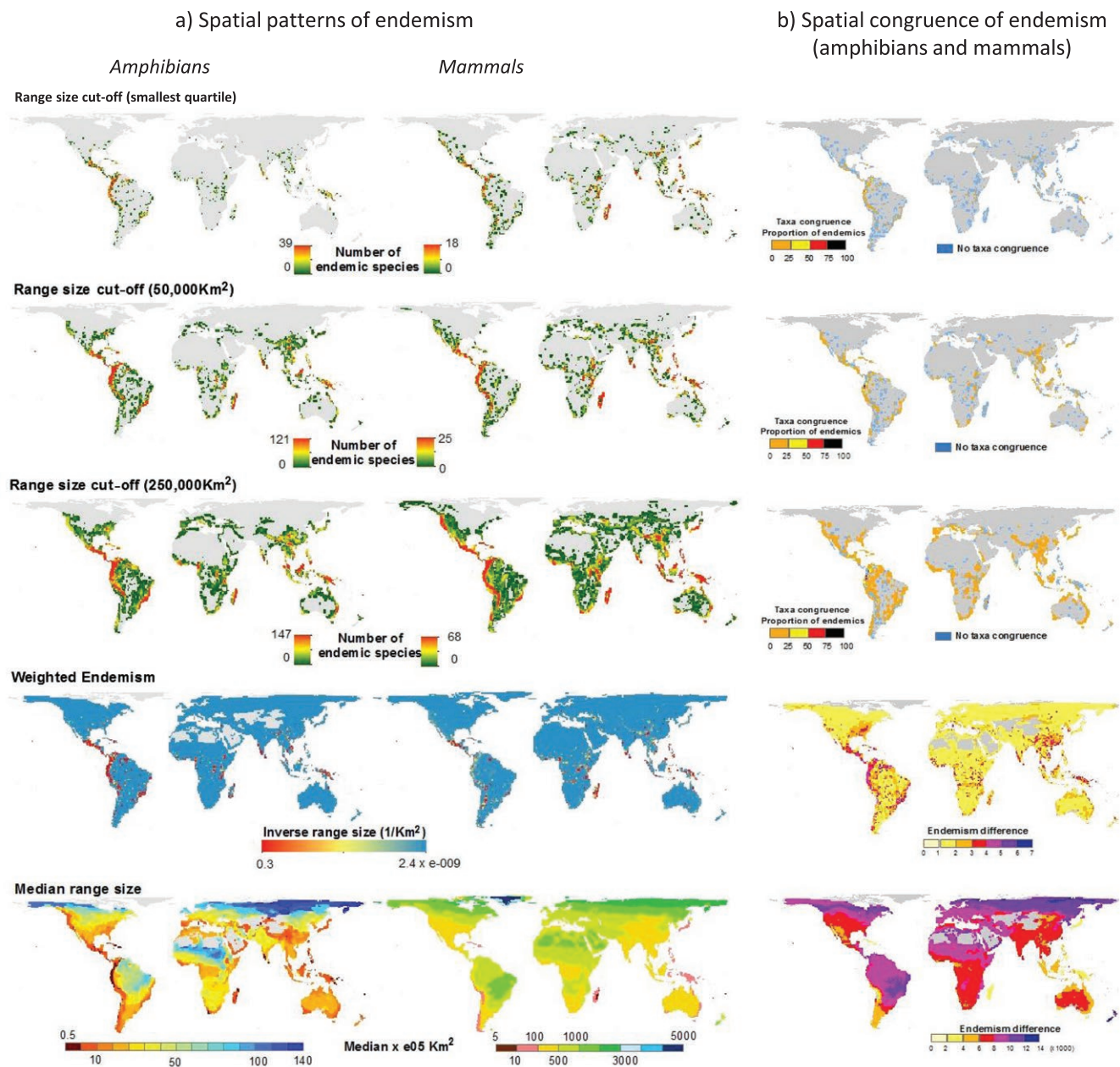

FIGURE 1 Broad-scale patterns of species endemism using five metrics; showing: (a) spatial distribution of mammal and amphibian endemism, and (b) areas of taxonomic congruence within major centres of endemism (i.e., overlapping areas of endemic species for mammals and amphibians at 100 × 100 km spatial resolution)

Information Figure S3). The most general pattern is that high numbers of range-restricted species of both taxa are found in tropical mountains, but the variation within mountainous regions is quite high (Supporting Information Figure S4a). Range-restricted species often occur in areas of complex spatial heterogeneity, but topographically complex places do not necessarily have higher richness of range-restricted species. Further, although range-restricted species often occur in mountainous environments they are also found at low elevations (Supporting Information Figure S4b). Finally, the proportion of species that are range restricted in areas of high species richness is highly variable, and it also depends upon the metric used to measure endemism (Supporting Information Figure S5).

3.2 | Metrics of endemism

Different metrics of endemism yield divergent patterns. Correlations among metrics of endemism vary considerably (amphibians $|r|$ = 0.29–0.839; and mammals $|r|$ = 0.295–0.859; Table 1a,b). Median and WE showed more spatial similarities ($|r|$ = 0.731 and 0.685 for amphibians and mammals, respectively). In addition, metrics of endemism were correlated with species richness (Table 1c), an effect that increased dramatically at coarser spatial resolutions (Supporting Information Figure S6).

3.3 | Preliminary considerations

Endemism among amphibians and mammals relates to all predictors (Supporting Information Table S1). However, the strength of the correlation varied among metrics and generally grew stronger as the range size cut-off increased. Similarly, the strength of correlations increased at coarser spatial resolution, although these relationships varied considerably (Supporting Information Tables S2 and S3). In addition, collinearities between some predictors (i.e., CV and SH_PET) tended to decrease at coarser spatial resolutions (Supporting Information Figures S7 and S8). Based on these results, we used for further analyses (model averaging and cross-validation) the finer spatial resolution (c. 110 × 110 km) and the smallest range size cut-offs for models that evaluated zero inflation.

For spatial heterogeneity, we decided to select the metric with the strongest statistical relationship between endemism and spatial heterogeneity (i.e., SH_PET). Standard deviation led to stronger statistical relationships with endemism, so variability of SH_PET is presented in standard deviation units. We assessed the coefficient of variation as an alternative measure for spatial heterogeneity but found that it was less effective than standard deviation-based measurements (Supporting Information Table S1). For climate seasonality, we also selected the metric with the strongest correlation coefficient (i.e., MATS). For climate distinctiveness, we selected CD_PT with an intermediate window and the smallest threshold, as correlations showed little variation among all alternatives (Supporting Information Tables S2 and S3).

3.4 | Weighted endemism

3.4.1 | Model averaging and path analysis

Models averaging showed that endemism for amphibians and mammals, across all ZRs, was best predicted by full set of predictors (including CV, MATS, SH_PET, and Richness), except for climate distinctiveness (CD_PT, see Table 2). Standardized coefficient estimates (which indicate effect size) showed that species endemism had the strongest relationship with Richness across all realms, a relationship that is stronger for amphibians (b = 0.37–0.71, Table 2) than for mammals (b = 0.11–0.43, Table 2). On the other hand, the effect sizes for SH_PET and CV were low for both amphibian and mammal species endemism ($b \sim |0.07$–$0.25|$). Variation partitioning showed that the variance explained by the global extent model was considerably higher for amphibians (R^2 = 0.72) than for mammals (R^2 = 0.08; Figure 2). Path analysis models (Figure 2) consistently showed that Richness directly related to endemism for both amphibians and mammals, although the model for mammals showed that its effect tends to disappear.

3.4.2 | Cross-validation

Cross-validation across ZRs showed that predictions of endemism systematically fail for both taxa (Figures 3 and 4). In most cases, low to moderate endemism is predicted reasonably well (except for Australian and Afrotropical ZRs). However, areas of high endemism are systematically under-predicted. RMSE values (a measure of prediction accuracy) for all ZR models were quite far from the expected minimum value of species endemism, indicating poor predictability of all models (Supporting Information Table S4). In general, models tended to better predict areas with low species endemism; however, areas with high species endemism are poorly predicted.

3.5 | Median range size endemism

These patterns differed substantially when we used median range size to measure species endemism. For example, SH_PET was the best predictor of endemism in both amphibians and mammals in all ZRs (Supporting Information Table S5). Meanwhile, the correlation between endemism and Richness and CD_PT were inconsistent (i.e., amphibian and mammal endemism displayed contrasting positive versus negative effects with these two predictors), CV responded inconsistently within ZRs and MATS emerged as an important predictor. With this metric of endemism, explained variance was comparable for mammals and amphibians (R^2 = 0.34–0.40). Path analysis showed stronger effects of SH_PET and MATS relative to Richness on endemism (Supporting Information Figure S9). Cross-validation across ZR boundaries, however, also failed consistently to predict endemism for either taxon (Supporting Information Figures S10 and S11, Table S6).

Our results were qualitatively similar after accounting for spatial autocorrelation using SAR models (Supporting Information Figures S12–S14).

TABLE 1 Spearman's rank correlation coefficients among (a) metrics of endemism for amphibians, (b) metrics of endemism for mammals, and between (c) total species richness and five metrics of endemism (including all 10,445 grid cells as sampling units at resolution of *c.* 110 × 110 km)

(a) Correlation coefficients among metrics of amphibian endemism				
	First quartile	50,000 km²	250,000 km²	WE
50,000 km²	0.537			
250,000 km²	0.423	0.765		
WE	0.413	0.708	0.839	
Median	−0.279	−0.485	−.611	−0.731
(b) Correlation coefficients among metrics of mammal endemism				
50,000 km²	0.731			
250,000 km²	0.501	0.665		
WE	0.549	0.683	0.859	
Median	−0.295	−0.391	−0.517	−0.685

(c) Correlation coefficients between endemism and total species richness		
Metric of endemism	Amphibian total richness	Mammal total richness
First quartile	0.29	0.31
50,000 km²	0.48	0.36
250,000 km²	0.61	0.55
WE	0.85	0.74
Median	−0.40	−0.34

Note. Metrics of endemism were constructed using range size cut-offs (first quartile, 50,000 and 250,000 km²), inverse range size (weighted endemism, WE) and median range size (Median). Note that the negative correlations involving Median are expected: larger median range size implies fewer range-restricted species.

3.6 | Two-part models: addressing zero-inflation

3.6.1 | Model fitting

Performance between hurdle and ZI models varied widely, although they were clearly different from the Poisson models (Supporting Information Table S7). There was no unequivocal evidence that zeroes originated from a single process (as expected from hurdle models). Both hurdle and ZI models accounted reasonably for observed zero counts.

3.6.2 | Cross-validation

Neither technique reliably identified areas with no endemic species in cross-validations across ZR boundaries. Most importantly, they similarly failed to identify areas of high endemism in those cross-validations (Supporting Information Figures S15 and S16 and Table S8). Hurdle models also differed among ZRs and did not reliably predict patterns of endemism in independent regions.

4 | DISCUSSION

There is no empirical reason, from the standpoint of model fitting, parameter estimates and model validation, to claim that any of the hypotheses or a combination of them (*H1*, *H2*, *H3* or *H4*) adequately account for broad-scale patterns of species endemism among mammals and amphibians. Although many relationships are statistically significant, and the variance explained is between low and moderate, more importantly, cross-validation across ZRs leads to significant differences between observations and predictions. In other words, it is sometimes possible to fit patterns of endemic species to variation in predictor variables, but those models do not predict endemic species numbers in independent data. Misspecification of models most likely arises from the omission of key variables (variables left out of the model) driving endemism. That is, climate and topography may have a role, but other drivers not included in multiple models may have a stronger role in shaping broad-scale patterns of endemism. Our results also suggest that broad-scale patterns of endemism relate to climatic factors globally and within ZRs, but they are not the main drivers.

TABLE 2 Summary of multi-model averaging explaining (a) amphibian and (b) mammal total species endemism (weighted endemism, WE) as a function of several predictors

Dataset[a]	H1: Climate stability (CV)	H2: Climate seasonality (MATS)	H3: Climate distinctiveness (CD_PT)	H4: Spatial heterogeneity (SH_PET)	Richness	No. of models[b]
(a) Amphibians						
Global extent	-0.14 (-0.16 to -0.12) 1.00	-0.06 (-0.07 to -0.04) 1.00	-0.003 (-0.02 to 0.01) 0.29	0.24 (0.22 to 0.25) 1.00	0.69 (0.67 to 0.71) 1.00	2
Afrotropical	0.02 (-0.01 to 0.04) 0.48	-0.56 (-0.58 to -0.54) 1.00	0.19 (0.17 to -0.20) 1.00	-0.11 (-0.17 to -0.05) 1.00	0.37 (0.31 to 0.43) 1.00	2
Australian	-0.14 (-0.16 to -0.12) 1.00	-0.03 (-0.05 to -0.01) 1.00	0.01 (-0.003 to 0.02) 0.55	0.25 (0.24 to 0.27) 1.00	0.71 (0.69 to 0.73) 1.00	2
Nearctic	-0.14 (-0.16 to -0.12) 1.00	-0.06 (-0.08 to -0.05) 1.00	-0.02 (-0.04 to -0.01) 0.96	0.19 (0.18 to 0.21) 1.00	0.71 (0.69 to 0.73) 1.00	1
Neotropical	-0.19 (-0.21 to -0.17) 1.00	-0.08 (-0.10 to -0.06) 1.00	-0.02 (-0.03 to -0.002) 0.83	0.21 (0.19 to 0.23) 1.00	0.66 (0.64 to 0.68) 1.00	1
Oriental	-0.13 (-0.15 to -0.11) 1.00	-0.06 (-0.07 to -0.04) 1.00	-0.002 (-0.01 to 0.01) 0.96	0.25 (0.23 to 0.27) 1.00	0.70 (0.68 to 0.71) 1.00	2
Palaearctic	-0.23 (-0.25 to -0.20) 1.00	0.04 (0.02 to 0.05) 1.00	-0.003 (-0.02 to -0.01) 0.28	0.21 (0.18 to 0.23) 1.00	0.70 (0.68 to 0.72) 1.00	2
Panamanian	-0.14 (-0.16 to -0.12) 1.00	-0.05 (-0.07 to -0.03) 1.00	-0.002 (-0.02 to 0.01) 0.28	0.23 (0.22 to 0.25) 1.00	0.70 (0.68 to 0.72) 1.00	2
Saharo-Arabian	-0.14 (-0.16 to -0.12) 1.00	-0.03 (-0.05 to -0.01) 0.98	0.02(0.002 to 0.03) 0.83	0.23 (0.21 to 0.25) 1.00	0.69 (0.68 to 0.71) 1.00	1
Sino-Japanese	-0.13 (-0.15 to -0.11) 1.00	-0.06 (-0.08 to -0.04) 1.00	-0.01 (-0.02 to 0.007) 0.37	0.24 (0.22 to 0.25) 1.00	0.69 (0.67 to 0.71) 1.00	2
(b) Mammals						
Global extent	-0.07 (-0.10 to -0.03) 1.00	-0.08 (-0.10 to -0.05) 1.00	0.02 (-0.006 to 0.04) 0.52	0.11 (0.08 to 0.14) 1.00	0.11 (0.08 to 0.14) 1.00	2
Afrotropical	-0.15 (-0.18 to -0.13) 1.00	-0.44 (-0.45 to -0.42) 1.00	0.18 (0.16 to 0.19) 1.00	-0.16 (-0.23 to -0.11) 1.00	0.43 (0.38 to 0.49) 1.00	1
Australian	-0.14 (-0.17 to -0.12) 1.00	-0.21 (-0.23 to -0.19) 1.00	0.08 (0.07 to 0.10) 0.55	0.25 (0.23 to 0.28) 1.00	0.40 (0.38 to 0.43) 1.00	1
Nearctic	-0.15 (-0.18 to -0.13) 1.00	-0.27 (-0.29 to -0.25) 1.00	0.05 (0.04 to 0.07) 1.00	0.21 (0.18 to 0.23) 1.00	0.39 (0.37 to 0.41) 1.00	1
Neotropical	-0.17 (-0.20 to -0.15) 1.00	-0.26 (-0.28 to -0.24) 1.00	0.11 (0.09 to 0.13) 1.00	0.20 (0.18 to 0.23) 1.00	0.30 (0.28 to 0.33) 1.00	1
Oriental	-0.15 (-0.17 to -0.13) 1.00	-0.27 (-0.29 to -0.25) 1.00	0.09 (0.08 to 0.11) 0.27	0.25 (0.22 to 0.27) 1.00	0.31 (0.29 to 0.33) 1.00	1
Palaearctic	-0.22 (-0.25 to -0.19) 1.00	-0.13 (-0.19 to -0.11) 1.00	0.10 (0.08 to 0.12) 0.28	0.19 (0.16 to 0.22) 1.00	0.32 (0.30 to 0.35) 1.00	1
Panamanian	-0.16 (-0.18 to -0.14) 1.00	-0.26 (-0.28 to -0.24) 1.00	0.09 (0.08 to 0.11) 0.28	0.23 (0.21 to 0.25) 1.00	0.32 (0.30 0.34) 1.00	1
Saharo-Arabian	-0.17 (-0.20 to -0.15) 1.00	-0.28 (-0.30 to -0.26) 1.00	0.08 (0.06 to -0.09) 1.00	0.23 (0.21 to 0.25) 1.00	0.30 (0.28 to 0.32) 1.00	1
Sino-Japanese	-0.16 (-0.18 to -0.14) 1.00	-0.27 9 -0.29 to -0.25) 1.00	0.09 (0.07 to 0.11) 0.37	0.23 (0.21 to 0.24) 1.00	0.32 (0.30 to 0.34) 1.00	1

Note. CV = climate velocity; MATS = climate seasonality in mean annual temperature; CD_PT = climate distinctiveness in total precipitation; SH_PET = spatial heterogeneity in potential evapotranspiration; Richness = total species richness.

Parameter estimates (first value), confidence intervals (0.95, in parentheses), and predictors' relative importance (ranges from 0 to 1; being 1 the most important predictor). All estimates standardized and presented for the entire globe and for individual zoogeographical realms. [a]The global dataset comprised the whole extent of the dataset (including all 10,445 grid cells as sampling units for a spatial resolution of c. 110 × 110 km), and the Zoogeographic Realms (ZR) are based on Holt et al. (2013)). Colours indicate significant effects (*p* < 0.05): either positive (blue) or negative (red). [b]Number of best-fit models (ΔAIC < 2) from multi-model averaging.
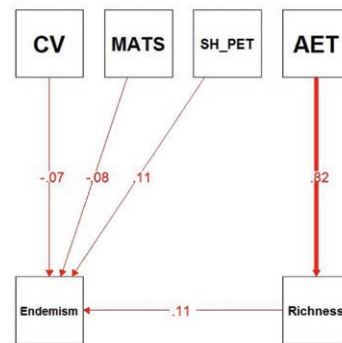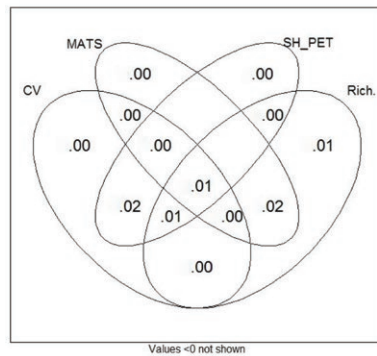
a) Amphibians
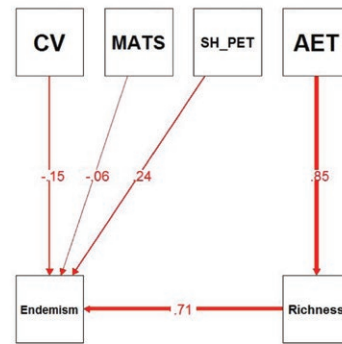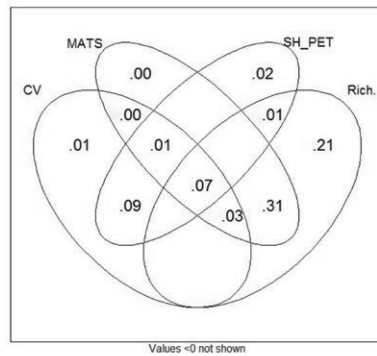
b) Mammals

FIGURE 2 Venn diagrams representing variance partitioning and path analyses representing the strength of the relationships for (a) amphibian and (b) mammal weighted endemism (WE) with various predictors using the global dataset (including all 10,445 grid cells as sampling units at a spatial resolution of *c*. 110 × 110 km). Climate velocity (CV), mean annual temperature seasonality (MATS), spatial heterogeneity in potential evapotranspiration (SH_PET), total species richness (Rich.) and actual evapotranspiration (AET) are included

It seems likely that the relationship between endemism and climate stability results from collinearity between climate stability and spatial heterogeneity in climate. The effect of SH_PET was larger than CV and it was more consistent among geographical regions. Two-part models (full models and those including only climate stability) significantly under-predicted species endemism (i.e., areas predicted to have no endemic species instead had many). This suggests that climate stability likely contributed little to losses of endemic species from areas where past climate changes were substantial (although usually far more gradual than present-day climate change). In other words, our results are not consistent with the hypothesis that extinctions occurred commonly in areas of high climate velocity (in geological terms) because species in those areas failed to track shifting climatic conditions (Sandel et al., 2011). It is likely that biological responses to post-glacial climate changes are primarily through changes in species abundance and distributions (Nogués-Bravo et al., 2016), rather than through massive extinctions of species. Small populations of at least some long-lived species may have persisted in refugia through periods of adverse climatic conditions (Willis & MacDonald, 2011).

Although seasonality can influence processes generating endemism, models including seasonality showed that its role is very marginal. This mechanism was thought to be amplified in mountainous regions at low latitudes, (Janzen, 1967). However, recent evidence shows that thermal barriers limiting organismal dispersal are similarly present in temperate realms (Zuloaga & Kerr, 2017), challenging the idea that this mechanism operates more in tropical regions. Despite the coincidence of some areas of endemism with rare climates, models showed that the relative effect size is systematically negligible across all ZRs, suggesting that rare climatic combinations do not play a leading role in creating or maintaining patterns of endemism.

Spatial heterogeneity in habitat was systematically one of the strongest predictors of endemism in all models. Our results are in line with previous research showing that endemic species are *often* found in mountainous regions (high spatial heterogeneity in habitat; Fjeldså, Bowie, & Rahbek, 2012) but not *exclusively* so. Spatial heterogeneity may contribute to broad-scale patterns of species endemism within regions, but it does not do so consistently among regions, even when heterogeneity is similar across disparate areas. The effect of spatial heterogeneity on endemism probably results from an interaction with some other variable.

Gradients of species endemism can be clearly distinguished from underlying gradients of species richness, suggesting that these fundamental biogeographical patterns arose globally from different processes. That models incorporating richness explained little variance in endemism for mammals (except for metrics that are by nature
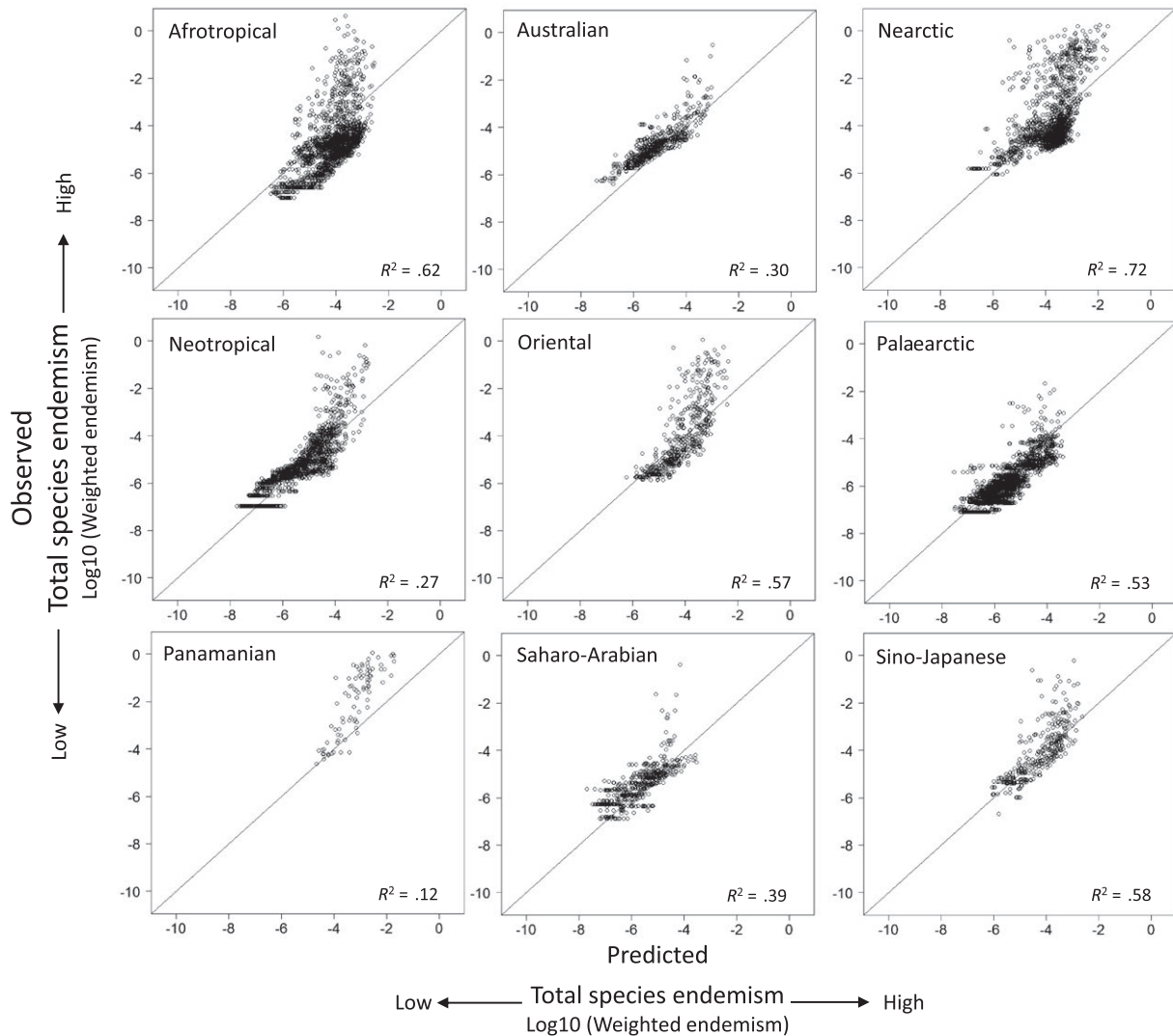
FIGURE 3 Observed versus predicted values of broad-scale patterns of amphibian weighted endemism (Log_{10}WE) using the cross-validation approach [i.e., models used data from all zoogeographical realms from Holt et al. (2013), excluding one, to predict endemism in the excluded zoogeographical realm, ZR]. We tested four hypotheses (predictors): *H1: Climate stability* (climate velocity); *H2: Climate seasonality* (seasonality in mean annual temperature); *H3: Climate distinctiveness* (in total precipitation, CD_PT); and *H4: Spatial heterogeneity* (in potential evapotranspiration, SH_PET); and added species richness as a covariate. Spatial resolution of *c.* 110 × 110 km. Results are for ordinary least squares (OLS) models. R^2 = coefficient of determination

correlated with Richness) and that their effects tend to disappear in path analyses reinforces the idea that species endemism is not a consequence of processes creating patterns of total species richness. Although global gradients of species richness relate to historical area, productivity dynamics and contemporary climate in consistent ways (Jetz & Fine, 2012), our results suggest that processes creating and maintaining broad-scale patterns of endemism must be decoupled from those of species richness.

If the hypotheses tested here do not explain the origin and maintenance of broad-scale patterns of endemism and those patterns are substantially decoupled from processes generating present-day gradients of species richness, how can endemic species diversity gradients be explained? Our models might have failed to predict observed patterns of endemism if other critical processes

were omitted from them. If these factors operate locally and do not relate consistently to environmental metrics, whether those are contemporary or historical, then the analyses performed here would not detect such effects. Some species' responses to climate are strongly scale-dependent (Schweiger & Beierkuhnlein, 2016). Even though the effects of abiotic factors on species richness are most readily detectable across broad areas (Willis & Whittaker, 2002), climatic conditions interact with highly localized habitats in ways that may shape species distributions and persistence (Lennon, Beale, Reid, Kent, & Pakeman, 2011; Opedal, Armbruster, & Graae, 2015; Sunday et al., 2014). Microclimates reduce species' exposure to broad-scale climatic trends that dominate a region, potentially permitting their persistence in areas that may be generally unsuitable (Maclean, Hopkins, Bennie, Lawson, & Wilson, 2015).
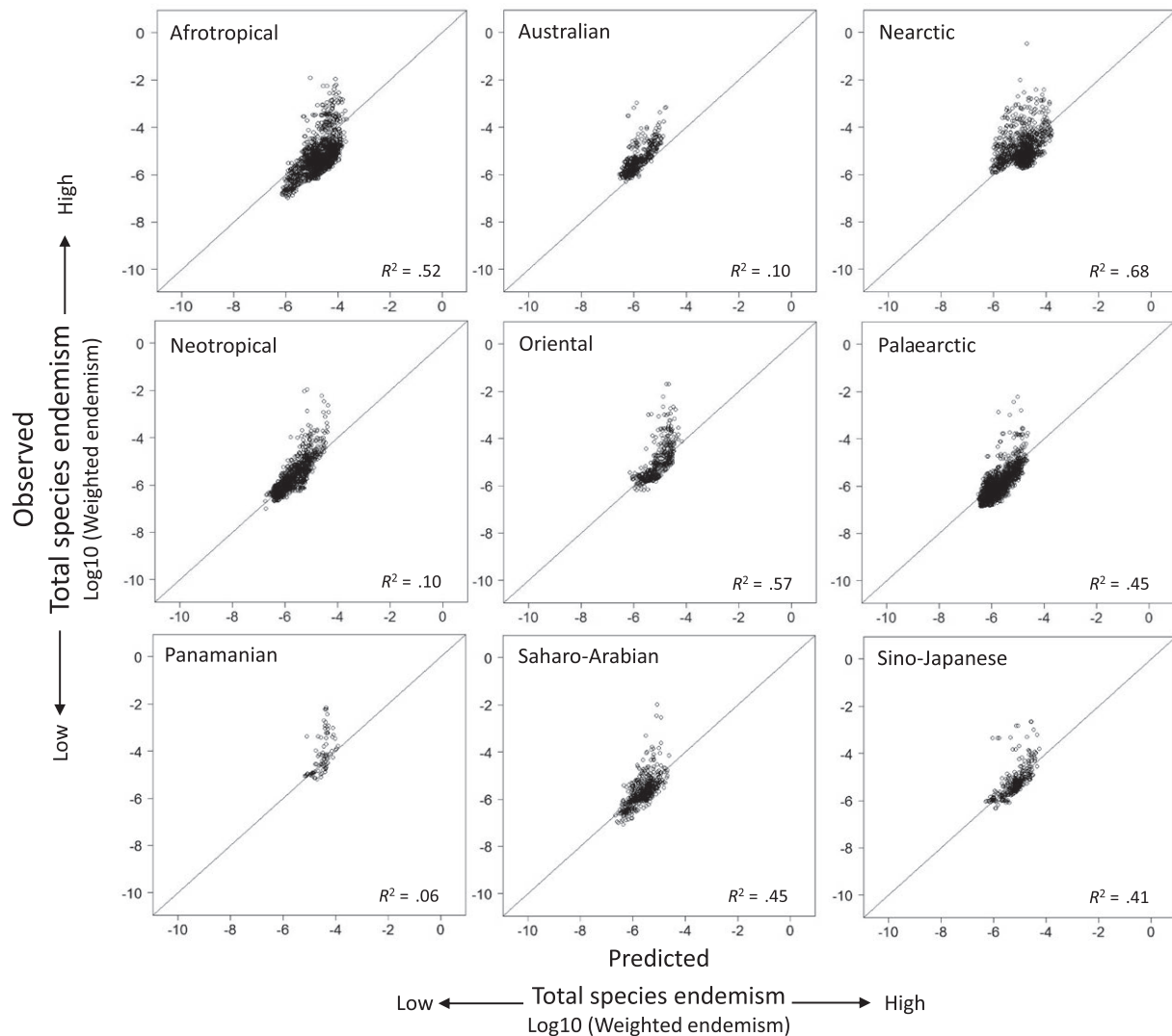
FIGURE 4 Observed versus predicted values of broad-scale patterns of mammal weighted endemism (Log$_{10}$WE), using our cross-validation approach [i.e., models used the data from all zoogeographical realms from Holt et al. (2013), excluding one, to predict endemism in the excluded zoogeographical realm, ZR]. We tested four hypotheses (predictors): *H1: Climate stability* (climate velocity); *H2: Climate seasonality* (seasonality in mean annual temperature); *H3: Climate distinctiveness* (in total precipitation, CD_PT); and *H4: Spatial heterogeneity* (in potential evapotranspiration, SH_PET); and added species richness as a covariate. Spatial resolution of *c.* 110 × 110 km. Results are for ordinary least squares (OLS) models. R^2 = coefficient of determination

Indeed, temperature, precipitation, and incident radiation can be modulated by topography and/or vegetation (De Frenne et al., 2013). Furthermore, biotic factors can strongly influence local species distributions (Jablonski, 2008), and some studies have shown macroecological signals of such species interactions (Gotelli, Graves, & Rahbek, 2010). Further research may integrate biotic factors including species interactions such as competition (Mordecai, Jaramillo, Ashford, Hechinger, & Lafferty, 2016), specialization (Fjeldså & Lovett, 1997), population and community dynamics (Locey & Lennon, 2016; Ralston, DeLuca, Feldman, & King, 2016), distributional shifts (Knowles & Massatti, 2017) and niche differentiation (Brown et al., 2013). A key question is whether and how such factors contribute to the origins and maintenance of species endemism in some areas and not in others that share similar environmental characteristics.

Region-specific peaks in endemism could also result from historical contingency, geographically distinct origins among continental biotas (Fjeldså, Ehrlich, Lambin, & Prins, 1997) and the presence of refugia during glacial maxima (Haffer, 1969; Rahbek et al., 2007). Dispersal ability is another intrinsic species trait that likely contributes to present-day species distributions (Leroux et al., 2013). Further research could usefully evaluate whether regional-specific historical factors, biotic origins, or isolation among phylogenetic lineages interact with the hypotheses tested here or alter patterns of endemism. Lack of congruence of patterns of species endemism between taxonomic groups also suggests that such processes are taxon-specific in their potential effects.

Methodological challenges complicate efforts to distinguish historical and contemporary influences on endemism. We have demonstrated that these obstacles can be overcome to enable clear tests

of causal hypotheses. Challenges include: (a) the spatial resolution of the analysis (Buckley & Jetz, 2008); (b) the nature of metrics used to measure species endemism (Crisp et al., 2001); (c) collinearity among predictors (Dormann et al., 2013); (d) the unusual statistical properties of spatial patterns of species endemism, such as zero inflation (i.e., excess of zeros in datasets; Martin et al., 2005); and (e) the strong correlation between metrics of species endemism and species richness that result from how endemism is measured and how metrics are corrected for this effect (Crisp et al., 2001). In addition to these issues, conclusions around the roles of any of these hypotheses in shaping gradients of endemism typically emphasize statistical significance of models or the strength of observed signals (variance explained), rather than the capacity of models to predict endemism in spatially independent areas, like ZRs.

Generation of accurate predictive models on how species might persist at small population sizes and in spatially restricted areas is needed to improve predictions for how changing environmental conditions (local and global) will affect the origins and maintenance of the world's centres of endemism. Models from the macroecological hypotheses tested here fail stringent tests, suggesting that we do not yet have a critical understanding of the origins and maintenance of global gradients of endemism.

ACKNOWLEDGMENTS

DATA ACCESSIBILITY

The datasets used for this analysis are freely available and can be accessed online as described below.

Worldwide species distribution maps for terrestrial mammals and amphibians are published by the IUCN (https://www.iucnredlist.org/technical-documents/spatial-data).

Climate data are available from WorldClim (https://www.worldclim.org/bioclim).

Potential evapotranspiration (PET) and the global dataset of yearly actual evapotranspiration are available from the Food and Agriculture Organization of the United Nations (https://www.fao.org/geonetwork).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.