



Differential effects of environmental heterogeneity on global mammal species richness

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ABSTRACT

Aim Spatial environmental heterogeneity (EH) is an important driver of species richness, affecting species coexistence, persistence and diversification. EH has been widely studied in ecology and evolution and quantified in many different ways, with a strong bias towards a few common measures of EH like elevation range. Here, we calculate 51 measures of EH within grid cells world-wide across three spatial grains to investigate similarities and differences among these measures. Moreover, we compare the association between species richness of terrestrial mammals and each EH measure to assess the impact of methodological choices on EH–richness relationships found by standard macroecological modelling approaches.

Location Global.

Methods We derive 51 measures of EH from nine variables related to the five subject areas land cover, vegetation, climate, soil and topography, using nine calculation methods. We first explore differences among these EH measures with correlation and principal components analyses. We then analyse the relationship between mammal species richness and each EH measure alone and while accounting for effects of current climate, regional biogeographic history and human influence. We assess the impact of subject area and method of calculation of EH measures on model support using conditional inference trees.

Results Despite some redundancy, correlations ($r_s = -0.45$ to 1.00, median 0.35) and spatial patterns indicate clear differences between the EH measures. We find clear effects of subject area and calculation method on the importance of EH measures for mammal species richness. Measures of climatic and topographic EH and measures calculated as counts and ranges (as against, for example, coefficient of variation) receive particularly high model support across all spatial grains.

Main conclusions The outcome of broad-scale EH–richness studies is greatly determined by methodological decisions on calculation of measures and statistical analysis. These decisions should therefore be made carefully with regard to the hypothesis and mechanism of interest.

Keywords

Biodiversity, climate, grain size, habitat diversity, heterogeneity measures, macroecology, spatial scale, topography, vegetation structure.

INTRODUCTION

Spatial environmental heterogeneity (EH) is an important determinant of species richness world-wide (Tews *et al.*, 2004; Stein *et al.*, 2014). EH is thought to enhance species richness through three mechanisms, involving ecological, historical and evolutionary aspects: (1) increased variation in resources, structural complexity or environmental conditions should increase available niche space and thereby promote species coexistence (Tews *et al.*, 2004); (2) increased EH should enhance species persistence by providing shelter and refuges from adverse environmental conditions like glaciations (Svenning & Skov, 2007); (3) increased EH should increase the probability of species diversification through isolation or adaptation to diverse environmental conditions (Hughes & Eastwood, 2006).

The effect of EH on species richness through these mechanisms is difficult to assess, as EH cannot be measured in any single, straightforward way. In fact, EH has been quantified by many different measures related to land cover, vegetation, climate, soil and topography (henceforth called subject areas). Measures of EH have mostly been calculated as ranges (e.g. elevation range), counts and indices (e.g. the number or Simpson index of land-cover types), but other calculation methods like percentage and standard deviation (e.g. percentage of forest cover; standard deviation of soil pH) have also been used. More than 160 measures, with many variations, exist in the literature (Stein & Kreft, 2014). Because of their different calculation methods and underlying data, these measures represent different aspects of EH. For instance, range measures capture the length of environmental gradients, and may relate to spatial turnover of species with different environmental requirements. The most frequently used range measure, elevation range, is a broad proxy not only for climatic gradients and habitat turnover but also for refugial opportunities and isolation and diversification probabilities (Kallimanis *et al.*, 2010). Index measures contain information about the variability or configuration of environmental variables within study units. For instance, foliage height diversity or plant species diversity have been used to quantify structural complexity and diversity of vegetation as proxies for resource diversity and availability of resting, hiding and breeding sites (e.g. MacArthur & MacArthur, 1961). Indices of topographic EH considering slope, aspect or ruggedness relate more to microclimatic and edaphic conditions like insolation, wind exposure and drainage, and may thereby also refer to the availability of resting and foraging sites (Bouchet *et al.*, 2014). The relevance of EH measures to species richness also depends on spatial scale – measures of vegetation structure, for instance, are expected to be more useful at smaller scales, where niche differentiation and biotic interactions play larger roles. At larger scales, climatic and topographic measures of EH related to turnover and isolation should be more relevant (Rahbek & Graves, 2001; Field *et al.*, 2009).

EH–richness research is biased regarding the use of EH measures, as most studies use only few common measures such as elevation range and the number or diversity of land-cover types (reviewed in Stein & Kreft, 2014). While these measures

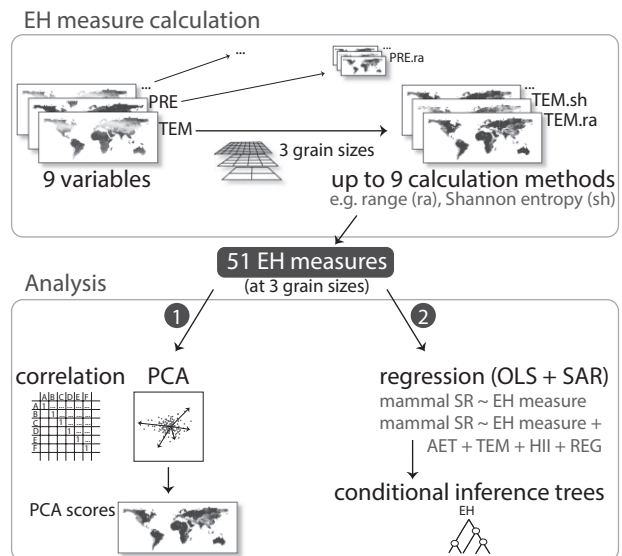


Figure 1 Schematic overview of the study design. Using nine variables and up to nine calculation methods per variable, we computed 51 environmental heterogeneity (EH) measures world-wide. Measure calculation and analyses were conducted within equal-area grid cells at three spatial grains (approximately 111 km × 111 km, 222 km × 222 km, and 444 km × 444 km). We (1) investigated the similarities among EH measures with correlation and principal component analysis (PCA), and (2) assessed the differences between EH measures in their association with species richness with ordinary least squares (OLS) and simultaneous autoregressive (SAR) models and conditional inference trees, using terrestrial mammals as case study.

are often easily available, they may miss important aspects of EH captured by other methods of calculation. Here we calculate a series of EH measures across three spatial grains world-wide, which cover different dimensions of biotic and abiotic EH by representing different calculation methods and all five subject areas (used in Stein & Kreft, 2014). We investigate the variability of these measures using correlation and ordination techniques and test how measures of EH vary in their association with terrestrial mammal species richness (see Fig. 1 for the study design). We are particularly interested in the impact of subject area and method of calculation of EH measures on study outcomes.

METHODS

Environmental data

Variables used for measures of EH

We derived EH measures representing five subject areas from nine variables thought to affect vertebrate species richness (e.g. Kerr & Packer, 1997; Fraser, 1998; Qian & Kissling, 2010).

1. Land-cover EH representing spatial turnover in environmental conditions: (a) land-cover classes (GLC; JRC, 2003); (b)

annual net primary production (NPP; 0.1 g C m^{-2} ; averaged over 2000–12; Zhao & Running, 2010).

2. Vegetation EH as proxy for vegetation structure and resource diversity: (a) vascular plant species richness based on kriging interpolation (PLA; Kreft & Jetz, 2007); (b) canopy height (VEG; m; Simard *et al.*, 2011).

3. Climatic EH representing turnover in energy and water: (a) annual mean temperature (TEM; K; Hijmans *et al.*, 2005); (b) annual precipitation (PRE; mm; Hijmans *et al.*, 2005); (c) mean annual potential evapotranspiration (PET; mm; Trabucco & Zomer, 2009).

4. Soil EH representing direct effects and indirect effects through vegetation: major soil groups (SOI; FAO/IIASA/ISRIC/ISSCAS/JRC, 2012).

5. Topographic EH as proxy for climatic gradients, habitat turnover and isolation probabilities: elevation (ELE; m a.s.l.; shifted to ≥ 0 by adding the absolute of the minimum, 431 m; Hijmans *et al.*, 2005).

All variables were resolved at 30 arcsec (approximately 1 km at the equator), except for PLA, which was resolved at approximately 111 km, the finest grain used in our analysis.

Calculation of EH measures

We calculated EH measures for global equal-area grid cells of $12,364 \text{ km}^2$ (approximately $111 \text{ km} \times 111 \text{ km}$ at the equator). To evaluate the influence of spatial grain on EH–richness relationships, we also calculated all measures at two coarser grains, i.e. grid cells of $49,457 \text{ km}^2$ (approximately $222 \text{ km} \times 222 \text{ km}$ at the equator) and $197,829 \text{ km}^2$ (approximately $444 \text{ km} \times 444 \text{ km}$ at the equator). PLA was the only exception; because area and species richness are not linearly related, to avoid additional assumptions we calculated PLA for the two coarser grains as mean plant species richness per grid cell based on the values at the finest grain. We focus on analyses at the 111-km grain, unless stated otherwise.

We applied nine calculation methods, chosen to capture different aspects of EH. For the categorical variables, GLC and SOI, we calculated three EH measures each: count (co; number of classes), Simpson index ($si = 1 - D$, where $D = \sum p_i^2$, with p_i being the proportion of the i th class) and Shannon entropy ($sh = -\sum p_i \ln p_i$). Higher EH estimated in this way is expected to promote spatial turnover of species with different habitat requirements. We also calculated these measures for continuous variables (NPP, VEG, TEM, PRE, PET, ELE) after classifying each variable into 50 equal-interval classes. To avoid spatial bias in these measures due to artificial class breaks, we shifted the breaks up and down seven times each (resulting in original breaks and seven up-shifted and seven down-shifted breaks). For each set of breaks, we recomputed the respective EH measure, and then used the mean of these 15 outcomes for analysis. Furthermore, we calculated the following measures for continuous variables: range (ra; max.–min.), standard deviation (sd), coefficient of variation (cv; set to zero for zero mean) and terrain ruggedness index (tr; mean per grid cell of the mean of absolute differences between the value of a pixel and the values

of its eight neighbouring pixels; Riley *et al.*, 1999). While ra measures cover the lengths of environmental gradients, the sd, cv and tr measures capture variability among sampling units. Tr is a proxy of terrain heterogeneity, designed to approximate structural attributes like cover for prey or predators (Riley *et al.*, 1999). For VEG, we additionally calculated the mean (me) and maximum (ma) canopy height, whereas we used PLA as an EH measure as it stands. We calculated 51 EH measures in total (Fig. 1), using R (R Core Team, 2013) and the packages *maptools*, *raster*, *rgdal*, *rgeos* and *vegan* (Bivand *et al.*, 2013; Bivand & Lewin-Koh, 2013; Oksanen *et al.*, 2013; Bivand & Rundel, 2014; Hijmans, 2014).

Further covariables

It is well documented that the species richness of terrestrial vertebrates strongly depends on current climate, particularly water and energy availability (e.g. Hawkins *et al.*, 2003; Qian, 2010). We therefore chose three climate variables known to affect broad-scale mammal richness (e.g. Qian, 2010; Davies *et al.*, 2011) to be accounted for in EH–species richness models, namely TEM, PRE and annual actual evapotranspiration (AET; mm; Ahn & Tateishi, 1994), which represents water–energy dynamics and is a proxy for productivity. For each variable, we calculated the mean per grid cell. AET was resolved at 30 arcmin only and was first disaggregated to 1 km. As AET and PRE were highly correlated ($r_s = 0.93$), we only included AET in our models, it being the most important predictor of mammal richness in several studies (Ruggiero & Kitzberger, 2004; Qian, 2010; Davies *et al.*, 2011). To account for regional and historical effects on mammal richness (see Hortal *et al.*, 2008), we also included seven mammalian biogeographic regions (REG; Kreft & Jetz, 2010) in our models. Finally, we included the global human influence index (HII) to account for anthropogenic impacts (Sanderson *et al.*, 2002; WCS & CIESIN, 2005).

Mammal data

We used range maps for 5282 terrestrial mammal species (IUCN, 2013), including historical ranges of (probably) extant and (possibly) extinct species and species with uncertain presence. We excluded introduced and vagrant species and species of uncertain origin. We calculated species richness for each grain as the number of ranges overlapping in each grid cell.

Statistical analysis

Many measures of EH correlate with area, impeding separation of the effects of EH and area per se (Triantis *et al.*, 2003; Stein *et al.*, 2014). We therefore aimed to keep the area of study units constant by excluding coastal cells and large inland water bodies. At the finest grain this left 8914 grid cells for which all environmental variables were available. The analyses conducted at the two coarser grains were based on 2003 and 399 grid cells, respectively.

We explored the similarity among EH measures using Spearman rank correlation and principal components analysis (PCA). As many EH measures were correlated, we analysed their effects on mammal richness in separate models. We first ran simple ordinary least squares (OLS) regressions between each EH measure and mammal richness. We also ran multi-predictor OLS models between each EH measure and mammal richness, adding AET, TEM, HII and REG as covariables. We compared these models with a model that included only AET, TEM, HII and REG as predictors of mammal richness, without an EH measure. Due to the large amount of variance explained by these four variables alone, and the acknowledged high importance of climatic and, to a lesser extent, regional effects for global mammal richness (Hawkins *et al.*, 2003; Hortal *et al.*, 2008), we used multi-predictor models in the remaining analyses. To examine the effect of spatial grain, all models were computed separately for the three grains. Mammal richness was square-root-transformed and several EH measures were log-transformed after data exploration (Table 1). If variables contained zero values, we added half of the smallest non-zero value before log-transformation. Models were computed with all variables standardized to zero mean, unit variance.

We detected considerable spatial autocorrelation in OLS model residuals inspecting Moran's *I*-based correlograms (Appendix S1 in Supporting Information). As spatial autocorrelation violates assumptions of independence and identical distribution of model residuals, it inflates Type I errors and may lead to biased model comparison and poor parameter estimates (Dormann *et al.*, 2007). We therefore accounted for spatial autocorrelation using simultaneous autoregressive (SAR) models of the error type, defining the neighbourhood structure based on the Akaike information criterion (AIC) and minimum residual spatial autocorrelation (Kissling & Carl, 2007). Spatial weights matrices for the three grains were based on row standardization and neighbourhood distances of 150, 300 and 550 km, respectively. This reduced residual spatial autocorrelation to negligible levels (Appendix S1). We calculated pseudo- R^2 values as the squared Pearson product-moment correlation coefficient between observed and predicted values separately for non-spatial and spatial terms (Kissling & Carl, 2007). SAR models were implemented with *spdep* (Bivand, 2014).

We compared the association of EH measures with mammal richness using the model AIC. As many measures of EH were correlated, we did not focus on the exact order of measures in the AIC ranking. Instead, using conditional inference trees (Hothorn *et al.*, 2006) we determined whether subject area or the method of calculation of EH measures was more important for SAR model support. In this binary recursive partitioning framework, tree splits are based on the strength of association between the response variable, i.e. Δ AIC of SAR models, and input variables, i.e. subject area and calculation method. In each step, the null hypothesis of independence between each input variable and the response variable is tested. The input variable having the strongest association with the response variable is selected according to the corresponding *P*-value, and in each step the data are split into two groups based on this input vari-

able. We implemented conditional inference trees with *party* (Hothorn *et al.*, 2006), using Monte Carlo testing and a stop criterion of 0.5. The splitting continued as long as $1 - P$ exceeded this stop criterion.

RESULTS

Measures of EH

We detected weak to strong collinearity among EH measures and even negative correlations, depending on the underlying variables and methods of calculation (Appendix S2). Spearman rank correlations ranged from -0.45 to 1.00 , with a relatively low median and mean of absolute correlations of 0.35 and 0.45 , respectively. Accordingly, global maps of EH measures revealed similar patterns in some cases (e.g. measures of ELE, PET and TEM; Appendix S3) but also clear differences (Fig. 2). While the Andean and Himalayan regions were characterized by high climatic and topographic EH (Fig. 2c,e, Appendix S3), large parts of Eurasia showed high GLC and SOI EH (Fig. 2a,d, Appendix S3). Measures of vegetation EH were particularly high in tropical South America, Southeast Asia and Central Africa (Fig. 2b, Appendix S3).

In the PCA of all 51 measures of EH, 70.7% of global spatial variation was accounted for by the first three principal components (Fig. 3, Appendix S4). The first component, accounting for 45.1% of the variation, mainly represented measures of climatic and topographic EH (Fig. 3a,b, Appendix S4). The second component (18.4%) was mainly positively correlated with measures based on NPP, PLA and VEG (Fig. 3a,c, Appendix S4), except for negative correlations with some cv and tr measures based on these variables. While the first component was positively correlated with mean elevation ($r_s = 0.48$), the second component was negatively correlated with mean elevation ($r_s = -0.44$) and positively correlated with mean AET ($r_s = 0.72$). Consequently, visualization of PCA space on global maps highlighted high mountain ranges for the first axis (Fig. 3d) and regions of high vegetation EH for the second axis (Fig. 3e). The third component (7.1%) was most strongly positively correlated with PRE measures and most strongly negatively correlated with GLC and SOI measures (Fig. 3b,c, Appendix S4). The associated map (Fig. 3f) opposed areas of particularly high PRE EH to areas of high soil EH.

The EH–richness relationship

Mammal richness ranged from 7 to 252 species per grid cell at the 111-km grain (10 to 277 and 12 to 336 species, respectively, at grains of 222 km and 444 km) and showed a pronounced increase towards the equator. The highest species richness occurred in the Andean and Afro-Montane regions, followed by Southeast Asia (Fig. 3j). Regions with high mammal richness coincided mainly with regions of high land-cover and vegetation EH and high values of PRE measures in PCA plots (Fig. 3g–i).

We found clear differences between single- and multi-predictor SAR models regarding the association of EH

Subject area	EH measure	Single-predictor SAR models			Multi-predictor SAR models		
		Δ AIC	R ²	b	Δ AIC	R ²	b
Land cover	GLC.co	861.61	0.03	0.05***	830.20	0.64	0.05***
	GLC.sh	795.90	0.04	0.05***	764.35	0.65	0.04***
	GLC.si	864.32	0.04	0.04***	837.99	0.65	0.04***
	NPP.co	257.67	0.45	0.12***	460.29	0.67	0.10***
	NPP.cv _{log}	1068.04	0.05	0.01***	1030.89	0.63	0.01***
	NPP.ra	468.12	0.46	0.10***	646.48	0.67	0.08***
	NPP.sd	309.48	0.28	0.07***	361.84	0.65	0.06***
	NPP.sh	412.81	0.30	0.10***	579.47	0.67	0.09***
	NPP.si	697.01	0.28	0.09***	798.47	0.68	0.07***
NPP.tr	1076.96	0.02	-0.00*	1054.46	0.63	0.00	
Vegetation	PLA.co	0.00	0.61	0.55***	423.22	0.72	0.46***
	VEG.co	403.12	0.45	0.09***	560.94	0.67	0.07***
	VEG.cv _{log}	1081.83	0.00	0.00	1053.61	0.63	0.00
	VEG.ma	502.52	0.45	0.09***	628.03	0.67	0.07***
	VEG.me	754.89	0.35	0.08***	889.67	0.64	0.06***
	VEG.ra	506.50	0.45	0.08***	625.61	0.67	0.07***
	VEG.sd	110.06	0.27	0.09***	277.72	0.66	0.08***
	VEG.sh	347.59	0.35	0.10***	618.43	0.67	0.08***
	VEG.si	587.20	0.32	0.09***	782.43	0.66	0.07***
VEG.tr	698.03	0.21	0.07***	837.88	0.64	0.05***	
Climate	PET.co	133.75	0.06	0.08***	72.21	0.65	0.08***
	PET.cv _{log}	611.28	0.00	0.06***	492.36	0.66	0.07***
	PET.ra	135.01	0.06	0.08***	74.06	0.65	0.08***
	PET.sd	436.03	0.05	0.06***	368.48	0.64	0.06***
	PET.sh	472.10	0.04	0.06***	416.52	0.64	0.07***
	PET.si	735.01	0.03	0.05***	709.67	0.65	0.04***
	PET.tr _{log}	342.81	0.10	0.09***	290.91	0.64	0.09***
	PRE.co _{log}	118.43	0.44	0.10***	342.73	0.65	0.08***
	PRE.cv _{log}	954.51	0.01	0.03***	921.86	0.63	0.02***
	PRE.ra _{log}	350.94	0.47	0.10***	495.42	0.68	0.09***
	PRE.sd _{log}	592.87	0.46	0.07***	695.22	0.66	0.06***
	PRE.sh	465.84	0.38	0.06***	658.83	0.63	0.05***
	PRE.si	655.94	0.44	0.05***	781.12	0.65	0.04***
	PRE.tr _{log}	246.41	0.36	0.11***	348.97	0.68	0.10***
	TEM.co	94.34	0.03	0.09***	3.84	0.65	0.09***
	TEM.cv	345.93	0.02	0.06***	272.38	0.64	0.06***
TEM.ra	91.32	0.03	0.09***	0.00	0.65	0.09***	
TEM.sd	317.33	0.02	0.06***	260.34	0.64	0.06***	
TEM.sh	395.97	0.01	0.07***	293.05	0.64	0.07***	
TEM.si	666.98	0.00	0.05***	609.73	0.64	0.05***	
TEM.tr _{log}	426.27	0.07	0.08***	378.49	0.65	0.08***	
Soil	SOI.co	879.91	0.00	0.03***	856.21	0.64	0.03***
	SOI.sh	945.14	0.00	0.02***	933.67	0.64	0.02***
	SOI.si	991.74	0.00	0.01***	977.40	0.64	0.01***
Topography	ELE.co	92.61	0.03	0.09***	3.35	0.65	0.09***
	ELE.cv	425.74	0.04	0.05***	531.07	0.65	0.04***
	ELE.ra	92.10	0.03	0.09***	1.40	0.65	0.09***
	ELE.sd	311.62	0.03	0.06***	270.80	0.64	0.06***
	ELE.sh	330.34	0.02	0.08***	227.64	0.64	0.08***
	ELE.si	616.35	0.01	0.06***	560.46	0.64	0.06***
	ELE.tr _{log}	501.08	0.06	0.08***	468.73	0.65	0.08***
Covariables only					1053.15	0.63	

Δ AIC (difference in the Akaike information criterion between each model and the best model), pseudo R² for the non-spatial model term and standardised regression coefficient b are given for each model. Significance levels: ***P = 0.001; *P = 0.05.

The 10 lowest Δ AIC values per model type are shown in bold.

Abbreviated EH measure names consist of three letters for variable and two letters for calculation method, for example ELE.sd, standard deviation of elevation.

Variables: ELE, elevation; GLC, land-cover classes; NPP, annual net primary production; PET, mean annual potential evapotranspiration; PLA, vascular plant species richness; PRE, annual precipitation; SOI, major soil groups; TEM, annual mean temperature; VEG, canopy height.

Calculation methods: co, count; cv, coefficient of variation; ma, maximum; me, mean; ra, range; sd, standard deviation; sh, Shannon entropy; si, Simpson index; tr, terrain ruggedness index.

Table 1 Single- and multi-predictor simultaneous autoregressive (SAR) models including environmental heterogeneity (EH) as a predictor of mammal species richness at 111 km × 111 km grain. Single-predictor models include one EH measure each; multi-predictor models include mean actual evapotranspiration, annual mean temperature, biogeographic region, human influence index, and one EH measure each (or no EH measure, i.e. *covariables only*). Mammal species richness was square-root-transformed; EH measures were log-transformed where indicated.

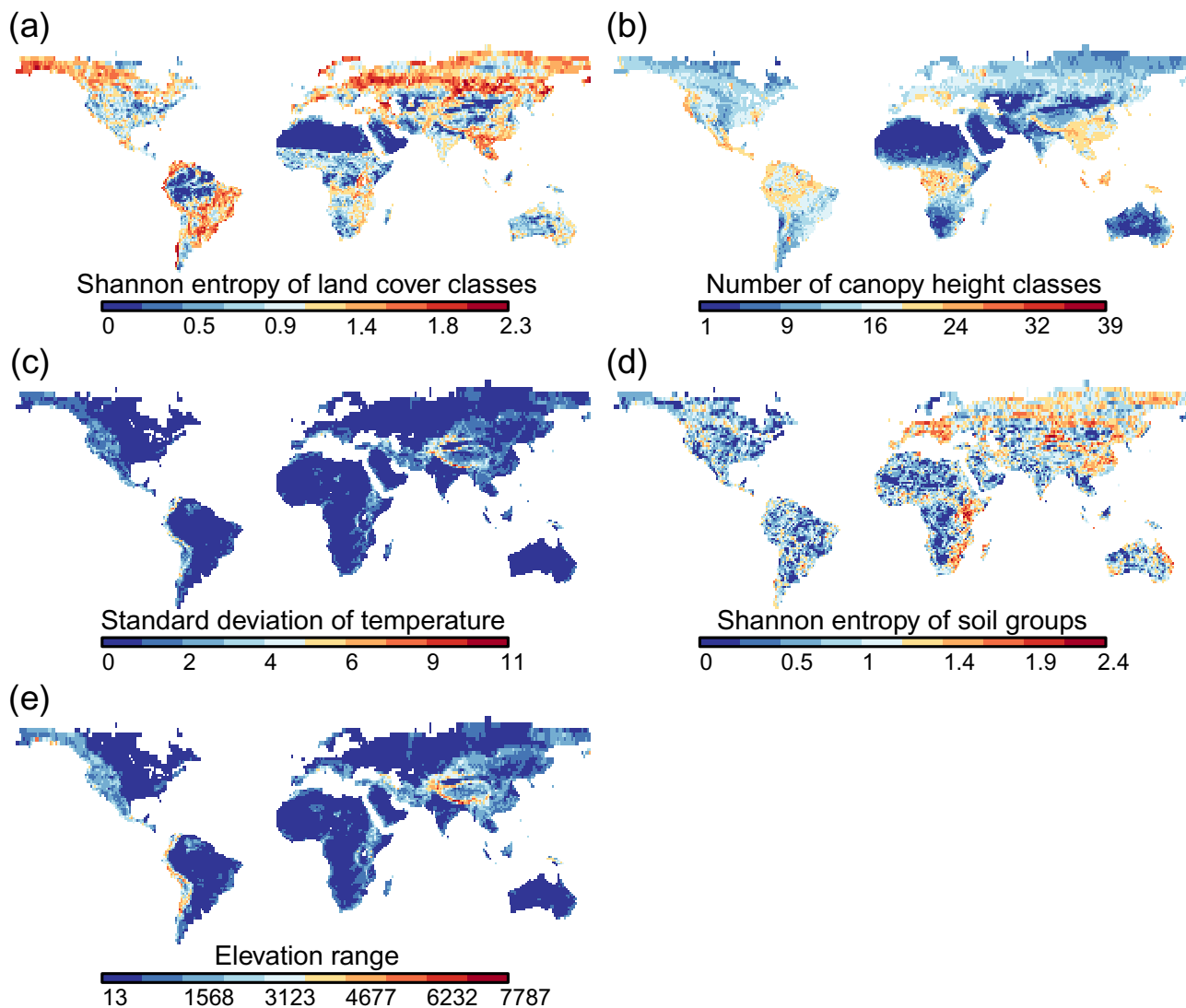


Figure 2 Selected maps of environmental heterogeneity (EH) measures at the 111 km \times 111 km grain; for a complete set of maps and additional grains see Appendix 3. (a) Shannon entropy of global land-cover classes; (b) the number of canopy height classes; (c) standard deviation of temperature; (d) Shannon entropy of major soil groups; (e) elevation range (m a.s.l.). Shades represent 10 equal-interval classes per EH measure according to the legends. Coastal cells and large inland water bodies were excluded to derive equal-area study units for analysis.

measures with mammal richness. In single-predictor models at fine spatial grain, PLA received by far the highest model support according to AIC, alone explaining 61% of the variation in mammal richness (Table 1). Next in AIC rank were the co and ra measures of TEM and ELE, but these models explained only 3% of the variation in mammal richness. While the number of precipitation classes gained highest support at the two coarser grains, the amount of variance explained and standardized regression coefficients for PLA remained high (Table 1, Appendix S5). Supporting our observations from PCA plots, other measures of vegetation EH and NPP also received relatively high support in single-predictor models, although they received lower support in multi-predictor models. The support for PLA was also much lower in multi-predictor models, in which measures of climatic and topo-

graphic EH had strongest support across all three grains. In particular, co and ra measures of TEM, PET and ELE had the highest model support. Measures based on PRE were also relatively well supported. The multi-predictor model that only accounted for AET, TEM, REG and HII without including EH explained 63–69% of the variation in mammal richness, depending on spatial grain (Table 1, Appendix S5). The amount of variation explained by EH measures alone in addition to the shared variance explained by the covariables ranged from 8–12%, being largest at the coarsest grain.

The differences in model support among EH measures were echoed by conditional inference trees, which revealed a significant split between EH subject areas in the first step (Fig. 4). Climatic and topographic EH were associated with the highest model support, i.e. the lowest Δ AIC values, across spatial grains.

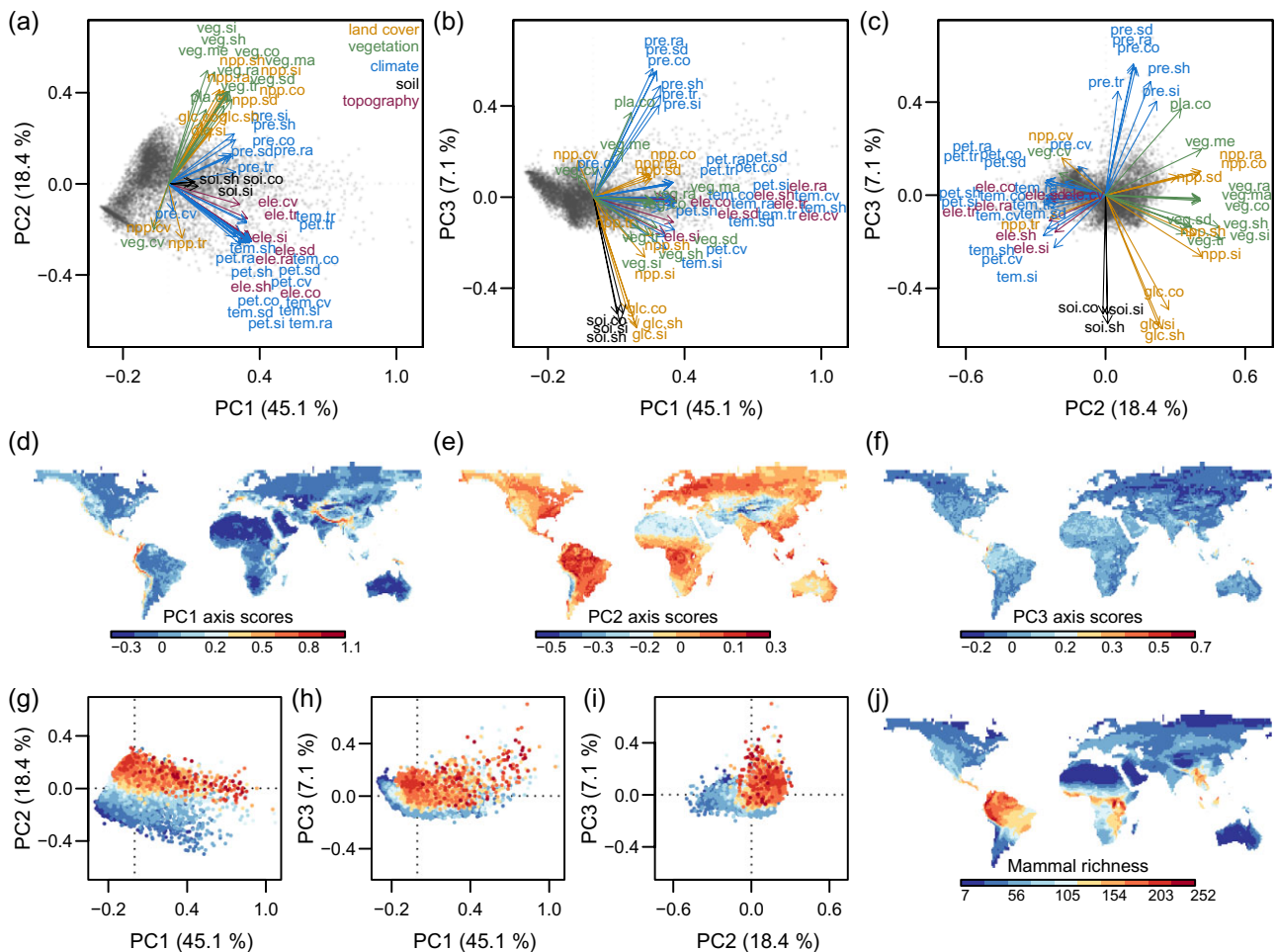


Figure 3 Principal components analysis (PCA) illustrating the variability and similarities among 51 measures of environmental heterogeneity (EH) at 111 km × 111 km grain. (a)–(c) The first three PCA axes with the percentage of variance accounted for by each axis given in parentheses. PCA points represent grid cells; abbreviated EH measure names (slightly shifted for clarity) consist of three letters for each variable and two letters for each calculation method, for example ELE.sd is the standard deviation of elevation. Variables: ELE, elevation; GLC, land-cover classes; NPP, annual net primary production; PET, mean annual potential evapotranspiration; PLA, vascular plant species richness; PRE, annual precipitation; SOI, major soil groups; TEM, annual mean temperature; VEG, canopy height. Calculation methods: co, count; cv, coefficient of variation; ma, maximum; me, mean; ra, range; sd, standard deviation; sh, Shannon entropy; si, Simpson index; tr, terrain ruggedness index. (d)–(f) Spatial visualization of PCA results. Shades of grid cells are based on PCA axis scores of the first three axes, representing 10 equal-interval classes per PCA axis according to the legends. (g)–(i) PCA as in (a)–(c), where PCA points are shaded according to mammal species richness in the relevant grid cells (legend in j). (j) Mammal species richness per grid cell (10 equal-interval classes).

At the coarsest grain, land-cover EH was also associated with higher model support than vegetation and soil EH (Fig. 4c). The second partitioning step separated calculation methods at all grains, but only for climatic, land-cover and topographic EH at the coarsest grain (Fig. 4). The co, ra and sd measures were among the best measures of EH, depending on the underlying variables and subject areas (Fig. 4, Appendix S5). EH measures based on cv, si and tr performed poorly overall, although tree splits for climatic and topographic EH at the finest grain had low significance (Fig. 4a).

DISCUSSION

We compared a wide range of measures of EH covering five subject areas, nine variables and nine calculation methods.

Besides some redundancies, we detected distinct differences between EH measures and their spatial patterns. We also found highly variable associations of EH measures with mammal richness, indicating that the choice of EH subject area and calculation method clearly affects study outcomes.

EH measures

The low correlations and spatial incongruence between several measures of EH confirms previous findings for topographic slope measures, i.e. that different calculation methods and data resolutions can yield varying results (Warren *et al.*, 2004). Different EH measures therefore capture different aspects of EH. Cv measures in particular were distinct from other calculation

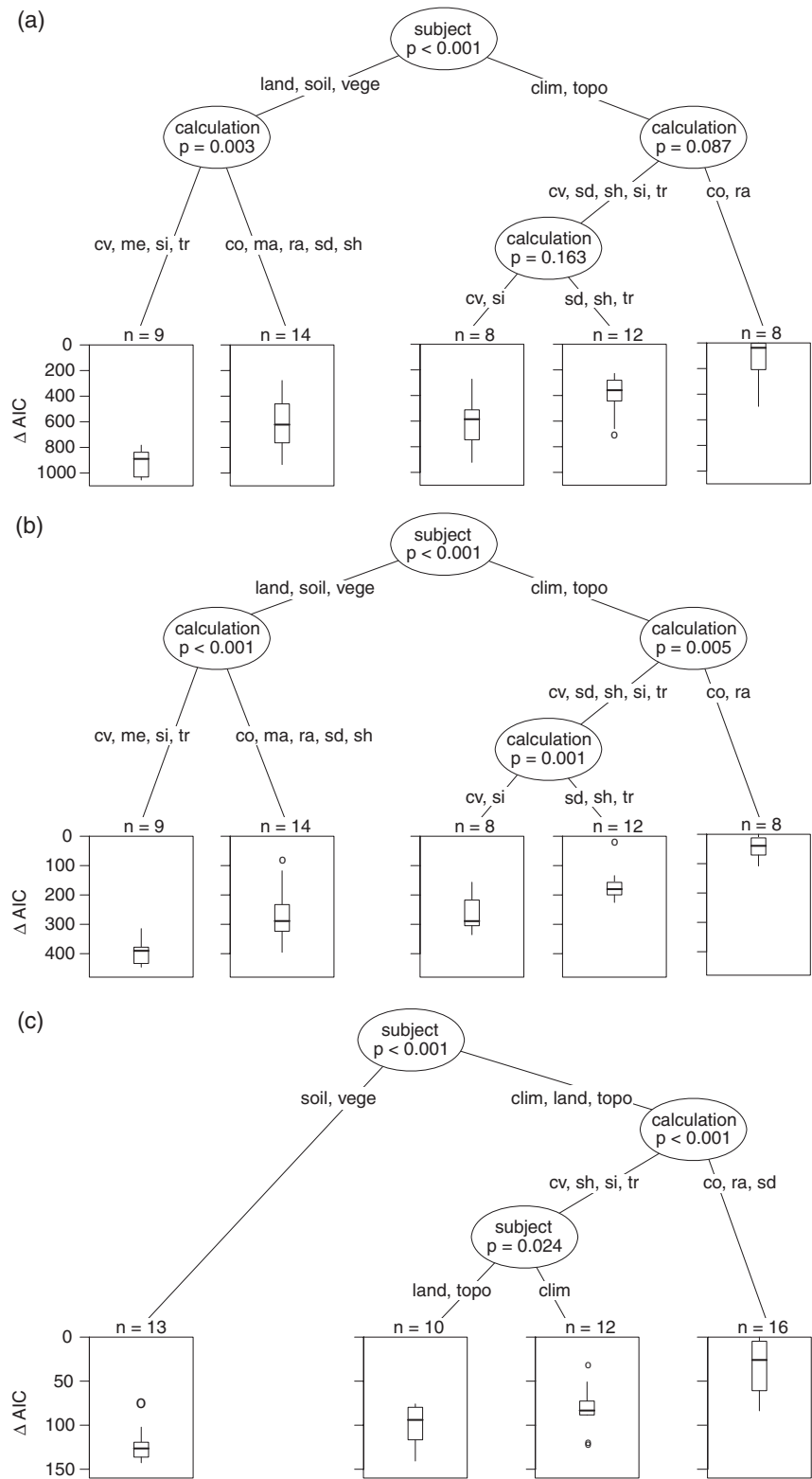


Figure 4 Conditional inference trees illustrating the effect of subject area and method of calculating environmental heterogeneity (EH) measures on ΔAIC -based model support in multi-predictor simultaneous autoregressive (SAR) models. Splits in conditional inference trees are based on the strength of association between the response variable, ΔAIC , and the input variables, subject area and calculation method. In each step the data are split into two groups based on the input variable with the strongest association with ΔAIC according to a P -value. Conditional inference trees are based on models from three spatial grains: (a) 111 km \times 111 km, (b) 222 km \times 222 km, (c) 444 km \times 444 km grid. Box-whisker plots represent the interquartile range around the median ΔAIC (boxes). Whiskers extend to extreme data points that are within 1.5 times the interquartile range from the box; circles represent outliers beyond this range. Abbreviations: subject, EH subject area; calculation, calculation method; clim, climatic EH; land, land-cover EH; soil, soil EH; topo, topographic EH; vege, vegetational EH; calculation methods: co, count; cv, coefficient of variation; ma, maximum; me, mean; ra, range; sd, standard deviation; sh, Shannon entropy; si, Simpson index; tr, terrain ruggedness index.

methods and negatively correlated with some EH measures, probably because low means of variables like NPP and VEG resulted in low ra and sd, but high cv values (e.g. in the Sahara; Appendix S3).

The close similarities among other EH measures (Appendices S2 & S3) make sense as many underlying variables are interde-

pendent, e.g. ELE, TEM and PET. A close relationship between vegetation structure and plant diversity, NPP and land-cover classes, as found here, is also expected based on theory and previous findings (e.g. MacArthur & MacArthur, 1961; Kissling *et al.*, 2008). Higher plant diversity is often associated with a more complex vegetation structure (MacArthur & MacArthur,

1961), while NPP and GLC are partly based on vegetation types. Similarly, several calculation methods are closely related to each other (consider, for example, elevation range and number of elevation classes). High collinearity has also been found for measures of topographic complexity involving elevation, slope and aspect, necessitating a careful selection of measures for analysis (Bouchet *et al.*, 2014).

The EH–richness relationship

Differences in model support among EH subject areas and between single- and multi-predictor models were striking. The exceptionally high amount of variance explained by PLA (61%), the strongest EH measure in single-predictor models, might be attributed to a functional response of mammal richness to higher resource diversity and structural complexity. However, the importance of vegetation EH clearly decreased in multi-predictor models, most likely due to adding AET as a covariable. PLA as well as *co* and *ra* measures of NPP were particularly strongly correlated with AET (r_s between 0.74 and 0.79; $r_s \leq 0.7$ for all other EH measures), making it difficult to tease apart their individual effects. AET is a strong predictor of global plant species richness (Kreft & Jetz, 2007). As it is also the main driver of broad-scale mammal richness (e.g. Ruggiero & Kitzberger, 2004; Qian, 2010; Torres-Romero & Olalla-Tárraga, 2015), AET probably captured much of the variation in multi-predictor models that was captured by vegetation and NPP EH in single-predictor models. The higher standardized regression coefficient of AET (median $b = 0.21$) compared with most measures of EH (median $b = 0.07$; Table 1) in multi-predictor models confirms the high importance of water–energy availability for mammal richness. A structural equation model suggests that the effect of PLA on mammal richness is mainly indirect and mediated by AET (Appendix S6). This confirms previous findings that broad-scale plant–mammal (Hawkins & Pausas, 2004) or, more generally, producer–consumer richness relationships (Jetz *et al.*, 2009) are mainly due to both groups responding to the same environmental gradients. However, direct effects of plant richness on mammal richness have also been found, varying in strength between spatial scales and mammal guilds (e.g. Qian *et al.*, 2009; Qian & Kissling, 2010). In addition to present-day ecological effects, PLA might also be related to mammal richness through co-evolutionary mechanisms (Jetz *et al.*, 2009). Disentangling ecological from historical and evolutionary mechanisms is a major challenge for future EH–richness research and should help to separate direct from indirect effects.

Measures of climatic and topographic EH gained high support in both single- and multi-predictor models. The fact that conditional inference trees generally favoured climatic and topographic EH over land-cover, soil and vegetation EH in the first tree split (Fig. 4) indicates that the choice of subject area affects model support more than the choice of calculation method. The importance of climatic EH for mammal richness is in line with the high importance of climate for broad-scale

vertebrate richness (Hawkins *et al.*, 2003; Field *et al.*, 2009). In contrast, few mammal species depend directly on specific soil types, for example for burrowing (Skinner & Chimimba, 2005), which probably explains the lower model support for soil EH. However, results could be biased in favour of climatic EH because sample size was higher than for the other subject areas (21 climatic EH, 10 land-cover and vegetation EH, 3 soil EH measures), as not all calculation methods could be applied to categorical variables and more meaningful variables were available for climate at a global extent. In contrast to climatic EH, topographic EH probably gained high model support because it incorporates multiple factors promoting species richness, including ecological, historical and evolutionary aspects. Firstly, topographic EH is a proxy for EH in various conditions that should foster species coexistence, including (micro-)climate, soil, hydrology and vegetation (Moeslund *et al.*, 2013; Bouchet *et al.*, 2014). Secondly, topographically heterogeneous areas promote species diversification and persistence through isolation and provision of refuges (Hughes & Eastwood, 2006; Svenning & Skov, 2007). The importance of climatic and topographic EH for species richness may, however, vary between regions in association with other variables such as energy availability, as shown for North American mammals (Kerr & Packer, 1997).

Interestingly, land-cover EH, which is frequently used in EH–richness studies, received less support than climatic and topographic EH, at least at the two finer grains. Theoretically, high land-cover EH promotes species richness, as it allows species with different habitat requirements to coexist (but see Allouche *et al.*, 2012). It is, however, difficult to define and measure habitat diversity, mostly because what is perceived as habitat varies strongly between organisms (Triantis *et al.*, 2005). A single land-cover classification as used here is unlikely to represent relevant habitat types for all studied mammal species. Furthermore, GLC and similar remote sensing datasets are not sufficiently resolved to reflect all (micro)habitats. It is therefore challenging to establish meaningful measures of land-cover EH at broad spatial and taxonomic scales.

Our findings certainly depend on the large spatial extent and grains of our analysis. Spatial extent affects the outcomes of species–richness research (e.g. Qian, 2010), and spatial grain greatly influences the measurability of EH and its importance for species richness (Whittaker *et al.*, 2001; Stein *et al.*, 2014). While we accounted for this by analysing three different grain sizes, the underlying data did not allow us to consider grains finer than 111 km. We expect climatic and topographic EH to become less important and vegetation and soil EH to become more important at finer scales, where climate and topography vary less and biotic interactions play a larger role (Pearson & Dawson, 2003; Field *et al.*, 2009). Previous smaller-scale studies found particularly strong effects of vegetation EH for mammal richness compared with climatic and topographic EH (Fraser, 1998; Qian & Kissling, 2010). Here, we found only minor differences between the analysed grain sizes, probably because all three were quite coarse. Still, multi-predictor models indicated an increasing trend in variance explained by EH with increasing

grain, consistent with previous findings (Fraser, 1998; Rahbek & Graves, 2001). Coarser grains have generally been found to be associated with stronger EH–richness relationships (Stein *et al.*, 2014), which makes sense because coarser grains usually entail larger within-cell variability in environmental conditions (Fraser, 1998). Additionally, allopatric speciation and species turnover mediated by EH should become more important drivers of species richness at coarser grains, whereas the adverse fragmentation effects associated with high EH may be most significant at fine spatial scales (Laanisto *et al.*, 2013). Also, the detected differences in model support between calculation methods may partly be explained by spatial scale. Co and ra measures appear to be useful proxies of EH at the broad scale studied here. In contrast, cv and si measures, which received low support in our study, have received high support for other variables and taxa at smaller spatial scales (e.g. Fraser, 1998; Ricklefs & Lovette, 1999). While spatial scales other than those studied here are thus likely to yield different results, the choice of EH measures should still play a crucial role in determining study outcomes.

We analysed all terrestrial mammals together; results from separate analyses of individual mammal groups would likely produce different results, as the strength of EH–richness relationships should depend on body size, range size, vagility, trophic group and habitat perception (Tews *et al.*, 2004; Triantis *et al.*, 2005). For instance, vegetation EH should particularly promote richness in arboreal and herbivorous mammals (e.g. Andrews & O’Brien, 2000). However, spatial scale is also likely to affect the outcomes of cross-group comparisons (Qian *et al.*, 2009), so generalizations should be made cautiously.

Although we calculated many measures of EH, more detailed indices and multivariate measures could be computed (e.g. McElhinny *et al.*, 2005; Bouchet *et al.*, 2014) that may be more comprehensive and informative about the underlying processes. Data availability for many more detailed measures, such as foliage height diversity, is thus far limited to small spatial extents, but advancements in remote sensing techniques might soon allow broad-scale calculation of measures of vegetation structure (Goetz *et al.*, 2010). While different measures of EH are expected to represent different mechanisms that influence species richness, it is hard to actually identify these mechanisms. As more detailed data become available, the use of measures that reflect actual functions of environmental variables, for example measures representing the effects of topographic EH on insolation or moisture, should promote greater understanding of EH–richness relationships (Moeslund *et al.*, 2013).

CONCLUSIONS

While some measures of EH are largely redundant, others exhibit strong spatial incongruence, making it worthwhile to include multiple measures in EH–richness research. EH and EH–richness relationships are inherently complex, and we showed that results of EH–richness analyses using common macroecological modelling approaches are sensitive to the choice of the method of calculation and the variable represent-

ing EH as well as to the statistical approach. Measures of climatic and topographic EH and count and range measures received the highest model support when accounting for effects of current climate, biogeographic region and human influence, thus representing more useful proxies of EH at a global extent and coarse grain than measures based on coefficient of variation or Simpson index. Measures of EH should be chosen carefully according to taxon, spatial scale, study system and mechanism of interest, and not merely based on convention or convenience. A selective comparison of multiple EH measures in the context of each EH–species richness study should promote better understanding and generalizations about the importance of EH for species richness.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

- Appendix S1** Spatial autocorrelation in model residuals.
- Appendix S2** Collinearity among measures of environmental heterogeneity.
- Appendix S3** Global maps of measures of environmental heterogeneity.
- Appendix S4** Results from principal components analysis.
- Appendix S5** Results from simultaneous autoregressive and ordinary least squares models.
- Appendix S6** Structural equation models of plant versus mammal species richness.

BIOSKETCH

The authors are interested in fine- to broad-scale ecology and biogeography. A particular interest lies in understanding environmental determinants of the species diversity patterns of various taxa, including plants, vertebrates and invertebrates.

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