Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales

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Abstract

Environmental heterogeneity is regarded as one of the most important factors governing species richness gradients. An increase in available niche space, provision of refuges and opportunities for isolation and divergent adaptation are thought to enhance species coexistence, persistence and diversification. However, the extent and generality of positive heterogeneity–richness relationships are still debated. Apart from widespread evidence supporting positive relationships, negative and hump-shaped relationships have also been reported. In a meta-analysis of 1148 data points from 192 studies worldwide, we examine the strength and direction of the relationship between spatial environmental heterogeneity and species richness of terrestrial plants and animals. We find that separate effects of heterogeneity in land cover, vegetation, climate, soil and topography are significantly positive, with vegetation and topographic heterogeneity showing particularly strong associations with species richness. The use of equal-area study units, spatial grain and spatial extent emerge as key factors influencing the strength of heterogeneity–richness relationships, highlighting the pervasive influence of spatial scale in heterogeneity–richness studies. We provide the first quantitative support for the generality of positive heterogeneity–richness relationships across heterogeneity components, habitat types, taxa and spatial scales from landscape to global extents, and identify specific needs for future comparative heterogeneity–richness research.

Keywords

Habitat diversity, habitat structure, meta-analysis, meta-regression, robust variance estimation, spatial scale, species diversity, topographical heterogeneity, vegetation structure.

Ecology Letters (2014)

INTRODUCTION

A major goal in ecology is to understand spatial patterns in the distribution of species diversity. Among the most important factors governing diversity gradients are contemporary factors such as ambient energy, water availability and productivity, area, biotic interactions and environmental heterogeneity, and factors related to historical processes such as phylogenetic niche conservatism and geological or climatic history (Currie 1991; Hawkins *et al.* 2003; Kreft & Jetz 2007; Field *et al.* 2009). In addition, a role of geometric constraints in shaping diversity gradients has been discussed (Colwell & Lees 2000). Spatial environmental heterogeneity (EH) is thought to promote species diversity through three major mechanisms: First, an increase in environmental gradients and in the amount of habitat types, resources and structural complexity should increase the available niche space and thus allow more species to coexist (e.g. Currie 1991; Tews *et al.* 2004). Second, environmentally heterogeneous areas are more likely to provide shelter and refuges from adverse environmental conditions and periods of climate change, which in turn should promote species persistence (e.g. Seto *et al.* 2004; Kallimanis *et al.* 2010; Fjeldså *et al.* 2012). Third, the probability of speciation events resulting from isolation or adaptation to diverse environmental conditions should increase with higher EH (e.g.

Rosenzweig 1995; Hughes & Eastwood 2006; Antonelli & Sanmartín 2011).

Widespread empirical evidence from many taxonomic and functional groups, geographical and ecological settings and spatial scales supports positive EH–diversity relationships (e.g. MacArthur & MacArthur 1961; Johnson & Simberloff 1974; Tews *et al.* 2004; Hortal *et al.* 2009). Several studies, however, have questioned the generality of positive EH–diversity relationships (e.g. Rohde 1992; Lundholm 2009) or have found non-significant or even negative effects (e.g. August 1983; Tamme *et al.* 2010; Gazol *et al.* 2013; Laanisto *et al.* 2013). Also, the existence of hump-shaped relationships caused by area–heterogeneity trade-offs, i.e. reductions in area suitable for particular species as EH increases, has recently been debated (e.g. Allouche *et al.* 2012; Carnicer *et al.* 2013; Hortal *et al.* 2013).

The role of EH in shaping richness patterns is particularly prone to controversy because of the high variability in research approaches and terminology, which may obscure the importance of EH in some study systems and impede generalisations from single studies (compare Box 1). EH incorporates heterogeneity in both biotic and abiotic conditions, which we classify into five subject areas: land cover and vegetation on one hand, and climate, soil and topography on the other hand (Box 1). Despite varying concepts and quantification methods, EH is assumed to have

a positive effect on richness, underlain by similar mechanisms, across studies and subject areas.

To understand the generality of ecological patterns, synthesis across spatial scales, taxa, realms and biomes is essential (Keith *et al.* 2012). Several review articles have treated the EH–diversity relationship, but they have often been restricted to a particular subject area or taxonomic group (Tews *et al.* 2004; Field *et al.* 2009; Hortal *et al.* 2009; Lundholm 2009; Tamme *et al.* 2010; De Araújo 2013). Furthermore, none of them has formally quantified the relationship across a wide range of taxa, while integrating both biotic and abiotic EH.

To broaden our understanding of the EH–richness relationship, we synthesised studies across taxa and subject areas using meta-analysis. Meta-analysis has become an important tool in ecology for generalising trends across studies and revealing overall patterns, even when single studies are too small or cover too narrow a range of conditions to detect an effect (Hillebrand & Gurevitch 2013; Koricheva 2013; but see Whittaker 2010). As the strength and direction of the EH–richness relationship are still debated, our meta-analysis aimed to reveal whether the relationship is generally positive and whether it varies systematically across terrestrial study systems and EH subject areas. We focused on landscape to global extents and aimed to answer the following questions: (1) Does the empirical evidence support the hypothesis that EH is, on average, positively associated with species richness? (2) What is the overall strength of the EH–richness relationship? (3) Is there significant variation in the relationship when considering different measures of EH, study taxa, locations and spatial scales?

Regarding the third question, our analysis was guided by the following hypotheses: (1) The importance of different components of EH differs among taxa. For instance, species richness of taxa depending directly on plants as resources should be affected more strongly by vegetation EH than by abiotic EH components, particularly at smaller spatial scales (Tews *et al.* 2004). Plant diversity should be particularly important for specialised herbivore richness (De Araújo 2013). (2) The effect of EH is stronger in regions with higher energy availability, where energy is not a limiting factor of species richness (Kerr & Packer 1997; Kreft & Jetz 2007). (3) The EH–richness relationship is scale dependent. The effect

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Box 1 Terminology and quantification of spatial environmental heterogeneity (EH)

The spatial heterogeneity, diversity and structure of the environment have been described by an astonishing number of terms. More than 100 different terms have been used in the literature, including e.g. altitudinal variation, elevational or environmental variability, habitat, landscape, or vegetation complexity/diversity/heterogeneity/structure, spatial heterogeneity/variability, structural complexity and many more. Terms are often only loosely defined or even defined and used differently by different authors. For instance, heterogeneity has been opposed to complexity as the horizontal vs. vertical component of habitat variation (August 1983), while others defined variability and complexity as components of heterogeneity (Li & Reynolds 1995). Habitat diversity has often been associated with the number of habitat types in a region, while habitat complexity or heterogeneity have often been related to within-habitat variability (e.g. August 1983; Hortal *et al.* 2009). Moreover, many authors have used multiple (sometimes up to ten) terms synonymously or without delimitation in a single study (e.g. Poggio *et al.* 2010). Clearly, this hampers understanding and cross-study comparisons. Even frequent terms such as habitat relate to different concepts and lack an unambiguous definition (Triantis *et al.* 2003). Here, we use environmental heterogeneity (EH) as an umbrella term for all terms relating to spatial complexity, diversity, heterogeneity, or structure in the environment. Although some of the above-mentioned terms have also been used to describe temporal heterogeneity in environmental conditions, there are fundamental differences between the concepts of temporal and spatial heterogeneity. Temporal heterogeneity generally considers the variation of resources and environmental conditions through time and is related to stability, predictability and stress (Menge & Sutherland 1976). It can be studied over short or long periods of time and from small to global scales. Often negative relationships between temporal heterogeneity (e.g. intra- and interannual seasonality in water availability, long-term climatic fluctuations) and species richness are assumed. Thus, we only consider spatial heterogeneity in our study.

Similar to the often inconsistent and confusing terminology, quantification of EH has been very diverse, not least because of the high variability in study systems, spatial scales and study taxa. The most frequently used measures for EH include elevation range, number or diversity of land cover types and number of plant species. But also these measures have many synonyms in the literature, impeding the finding of studies, understanding and synthesis. Furthermore, different measures may describe equivalent concepts in different studies, thereby making generalisations difficult: for instance, diversity in biotope, ecosystem, or habitat types relate to similar concepts, and the number of bird-dispersed vs. caterpillar food plant species both refer to food plant richness (e.g. Hawkins & Porter 2003; Kissling *et al.* 2007).

We classified EH measures into five subject areas (compare Table 1):

Biotic EH

Land cover EH refers to between-habitat heterogeneity, i.e. it is concerned with EH constituted by multiple habitat (or land cover/vegetation) types or patches.

Vegetation EH includes the physical structure of vegetation and its taxonomic or functional composition, i.e. plant diversity.

Abiotic EH

Climatic EH relates to spatial heterogeneity in micro- to macroclimatic conditions.

Soil EH incorporates e.g. heterogeneity in nutrients, acidity or diversity of soil types.

Topographic EH ranges from microtopographic structures to large-scale topographic relief.

of EH should increase with spatial grain, because larger sampling units generally include greater variability in environmental conditions (van Rensburg *et al.* 2002; Kallimanis *et al.* 2008). Moreover, EH should be more important at landscape scales, whereas climate and factors related to colonisation and extinction should dominate at large spatial extents (Rowe 2009; Qian & Kissling 2010). (4) Studies conducted using grain sizes of unequal area overestimate the influence of EH due to the confounding effect of area, as area and EH are often closely related (Rosenzweig 1995; Triantis *et al.* 2003).

METHODS

Study selection

We systematically searched the literature for studies investigating the relationship between one or more measures of EH and species richness. We applied three different approaches to detect as many studies as possible and reduce bias in data selection. First, we used the topic search in ISI Web of Science, including all years until April 2011, all languages and all document types. Our extensive search string contained 68 different terms for EH, such as 'habitat diversity', 'landscape complexity' and 'topograph* heterogeneity', in combination with '"species diversity" OR "species richness" OR "species number" OR "species density"'(see Appendix S1 for details and full search strings). Second, we screened the references included in several relevant reviews (Ricklefs & Lovette 1999; Tews *et al.* 2004; Field *et al.* 2009; Hortal *et al.* 2009; Lundholm 2009; Tamme *et al.* 2010). Third, we inspected the references cited by the articles found through the first two search modes.

Altogether, we reviewed titles, abstracts and in many cases the full text of 2236 articles for relevance and agreement with our inclusion criteria. Studies were included if they: (1) were observational, (2) examined terrestrial systems, (3) analysed species richness of plants or animals (i.e. the number of species, not a diversity index, as these two should not be combined in the same meta-analysis; Whittaker 2010), (4) quantified spatial EH, (5) covered a spatial extent of at least 10 km² in area or 10 km in distance, (6) provided summary statistics or raw data that could be converted into an effect size and (7) had a minimum sample size of four so that the variance of the effect size could be calculated. We excluded cases where the EH measure used quantified effects of anthropogenic disturbance (e.g. logging, grazing), as such studies only indirectly considered effects of EH and could not be classified into our five EH subject areas. We also excluded studies that only quantified EH through area or absolute elevation. Although area and elevation are often useful proxies for EH, they are also linked with other processes that impede inference of the effects of EH (see Triantis *et al.* 2012 for a recent review of island species–area relationships). When multiple studies analysed, even partly, the same data from the same location, we only included the most comprehensive data points in our analysis to avoid pseudoreplication. In some cases, when raw data on species richness and a common measure of EH were provided, we included

EH–richness relationships even when they were not discussed in the respective studies.

Data extraction

Statistical information on simple relationships between EH and species richness was extracted from text, tables or figures. When relevant statistics were not reported, we obtained raw data from tables or graphs (Engauge Digitizer 4.2; http://digitizer.sourceforge.net), where possible, to calculate correlations. In some cases, missing statistical information could be obtained from authors.

We recorded the following study characteristics, if available: (1) taxon: taxonomic group, trophic group, thermoregulation; (2) location: geographic coordinates, biogeographic realm and biome according to Olson *et al.* (2001), insularity, main habitat type; (3) methodology: whether the units of analysis were of equal area or not, spatial grain and extent, sample size (e.g. number of plots), EH measure and subject area. We classified measures within subject areas into EH measure categories so that they related to the same concept (Table 1). Many studies reported multiple EH–richness relationships, which we recorded as separate data points within each study. These were based on multiple study locations, taxa, spatial scales or EH measures.

If the information provided on study location and spatial scale was insufficient and could not be obtained from authors, we estimated study location coordinates and study areas using maps, other studies conducted at the same location, or study descriptions. We created spatial polygons for all data points, using minimum convex hulls to estimate missing spatial extents and centroids of the study areas. We calculated mean potential evapotranspiration (PET) for all study areas based on these polygons and the Global-PET Database (Zomer *et al.* 2008, http://www.cgiar-csi.org). We recorded spatial grain for all data points as the mean area of the units of analysis. All these study characteristics were used as covariates in the analysis except for thermoregulation, geographic coordinates and biogeographic realm and biome (see Table 2 for details). Geographical analyses were performed in ESRI ArcMap and R, packages *maptools* and *rgdal* (ESRI 2010; R Core Team 2013; Bivand & Lewin-Koh 2013; Bivand *et al.* 2013, respectively).

Statistical analysis

We used Fisher's *z* to quantify the effect size of EH–richness relationships. We derived *z* from correlation coefficient *r* using Fisher's *r*-to-*z* transformation (Shadish & Haddock 2009): $z = 0.5 \times \ln[(1 + r)/(1 - r)]$. This transformation is normalising and variance stabilising so that the variance v_z depends only on sample size *n* and not on the strength of the correlation itself (Shadish & Haddock 2009): $v_z = 1/(n - 3)$. We derived *z*-values from r^2 values of simple regressions or from *F*- and *t*-statistics following Rosenberg *et al.* (2000). As we were interested only in the simple relationship between EH and species richness, we did not include results from multiple regressions or partial correlations, where coefficients are affected by additional covariates, leading to poor comparabil-

Table 1 Subject areas of environmental heterogeneity (EH) categorised into EH measure categories relating to the same concepts with example measures used for quantification of EH

EH subject area	EH measure category	Example measures
Land cover	Land cover proportion	% Cover of forest; % cover of grassland
	Land cover diversity	# Land cover types; Shannon index of land cover types
	Patchiness	Edge density; mean patch size
Vegetation	Plant diversity	# Plant species; Shannon index of tree species
	Vegetation complexity	Foliage height diversity; PCA of vegetation variables
	Vegetation dimension	CV of trunk perimeter; density of plants
Climate	Climate	CV of precipitation; temperature range
Soil	Soil diversity	# Soil types; Shannon index of soil types
	Soil variables	CV of soil moisture; SD of soil pH
Topography	Elevation diversity	Elevation range; SD of elevation
	Microtopography	# Microtopographic elements; % cover of rocks
	Profile	SD of profile curvature; slope
Mixed	Mixed	Composite heterogeneity index; # ecological variables present

CV, coefficient of variation; #, number of; %, percentage of; PCA, principal component analysis; SD, standard deviation.

Table 2 Study characteristics included as covariates in meta-regressions

Variable	Type	Details
Equal area	cat	0 (109/434); 1 (85/714)
Spatial grain	con	m^2; log transformed
Spatial extent	con	km^2; log transformed
EH subject area	cat	Land cover (92/517); vegetation (68/315); climate (11/56); soil (16/37); topography (74/212); mixed (3/11)
EH measure category	cat	Land cover diversity (79/285); land cover proportion (19/108); patchiness (10/124); plant diversity (37/148); vegetation dimension (16/67); vegetation complexity (29/100); climate (11/56); soil diversity (10/25); soil variables (7/12); elevation diversity (67/178); microtopography (5/5); profile (7/29); mixed (3/11)
Habitat type	cat	Forest (57/367); mixed (91/475); non-forest (46/306)
Island	cat	0 (142/956); 1 (52/192)
Mean PET	con	mm/a; no transformation
Broad taxon	cat	Plants (67/336); invertebrates (56/289); vertebrates (85/523)
Fine taxon	cat	Plants (67/336); invertebrates (56/289); birds (54/284); herptiles (13/36); mammals (29/109); mixed vertebrates (3/94)

Details present factor levels of categorical (cat) variables with the according number of studies/data points in parentheses, and units and potential transformations for continuous (con) variables. Categories for equal area and island mean 'no' (0) and 'yes' (1). For a more comprehensive quantification of study characteristics, see Appendix S6.

ity across studies. We changed the sign of effect size estimates derived from EH measures where a higher value signified lower EH, e.g. percentage grassland cover.

The studies varied widely in their design, and we could not investigate the influence of all possible study characteristics on the EH–richness relationship. We therefore used a random-effects framework, where each study-specific true effect is subject to random variation (Viechtbauer 2007). This incorporation of between-study heterogeneity allows for generalisation to all potential studies (Hedges & Vevea 1998).

Many studies reported multiple outcomes that were non-independent, as a result of phylogenetic relatedness of species, spatial autocorrelation or nestedness, multiple measurements on the same community, or specific methods applied by a particular research team (compare Nakagawa & Santos 2012; Mengersen *et al.* 2013). Ignoring such dependencies would lead to an underestimation of standard errors, impaired statistical inference and a stronger weighting of studies that provide more outcomes (Borenstein *et al.* 2009). To our knowledge, our study is the first in ecology to use a recent method for robust variance estimation (RVE), which allows for meta-regression with dependent effect size estimates and

thereby the utilisation of all available study outcomes (Hedges *et al.* 2010).

To increase precision of summary effects, we weighted effect size estimates by their inverse variances, such that studies with higher sample sizes were given more weight (Borenstein *et al.* 2009). We used random-effects inverse variance weights as suggested by Hedges *et al.* (2010), where the total weight of any single study is bounded so that studies are not assigned more weight just because they provide more outcomes: $w_{ij} = 1/[k_j (v_{\bullet j} + \tau^2)]$; w_{ij}: weight of the ith effect size estimate in the jth study; k_j: number of effect size estimates in the jth study; $v_{\bullet j}$: unweighted average of the variances of effect size estimates in the jth study; τ^2: estimate of the between-study variance component. We used a value of 0.8 for the within-study correlation ρ, i.e. the mean correlation between all effect size estimates per study, to estimate τ^2. Sensitivity analyses indicated that our results are robust to variation in ρ (Appendix S2; compare Hedges *et al.* 2010).

We performed seven separate meta-regression analyses to study overall mean effects, compare different effects for biotic vs. abiotic EH, EH subject areas and measure categories and to test our hypotheses using three different subgroups of the

data. Based on an intercept-only model, we first estimated a weighted mean effect size with robust 95% confidence interval (CI; Hedges *et al.* 2010) for the complete data set. As we expected a significant influence of whether studies were based on equal-area units or not, we also estimated a weighted mean effect size for equal-area studies only. To test whether the strength of the EH–richness relationship differed between EH components, we ran three mixed-effects meta-regressions including biotic vs. abiotic EH, EH subject area or EH measure category as fixed effects. Differences between fixed-effect categories were determined using *t*-tests on meta-regression coefficients while changing the reference category level. Studies that used composite measures relating to more than one EH subject area (e.g. Harner & Harper 1976) were excluded from these meta-regressions. We also conducted the meta-regression with EH measure categories for equal-area studies only.

We tested our hypotheses further using three subgroups of the data, containing related EH measure categories or specific taxonomic groups. EH measure categories that were represented by < 20 studies were omitted (compare Tanner-Smith & Tipton 2014; López-López *et al.* 2014). Subgroup I contained the EH measure categories elevation diversity and land cover diversity, which are often used as proxies for the number and diversity of habitat types (but see Hortal *et al.* 2013). Subgroup II included the EH measure categories vegetation complexity and plant diversity. For these two subgroups, we examined multiple covariates simultaneously to account for correlations among covariates and thereby avoid confounding effects (Viechtbauer 2007). Hence, similar to other meta-analyses that have used RVE (e.g. Tanner-Smith *et al.* 2013),

we ran three consecutive meta-regressions. Model 1 tested whether methodological study characteristics affected the average effect size estimate. As spatial scale has often been shown to influence effect sizes (Chase & Knight 2013), we included spatial grain, extent and equal area in this model. Furthermore, we included EH measure category to account for differences in EH measurement. Model 2 tested the effect of the location-related covariates habitat type, mean PET and insularity, while accounting for study methodology. Model 3, the full model, tested the effect of taxon-related covariates, including either broad or fine taxonomic group, while also accounting for study methodology and location. Due to collinearity among covariates, we did not include insularity in the models of subgroup I or mean PET in the models of subgroup II (Appendix S3). As most studies analysed the effect of vegetation EH on animal richness, we excluded four data points examining the effect of EH on plant richness from subgroup II to allow for a meaningful test of taxonomic group. In models of subgroup I, we excluded two data points for which spatial extent was not available. We included all covariates as study-level means to allow the estimation of between-study effects. Subgroup I included 22 studies that each varied in spatial grain, so we additionally centred spatial grain around the study-level mean to test for within-study effects (Tanner-Smith & Tipton 2014).

We did not include trophic group in these meta-regressions due to collinearity among covariates and because many studies examined taxa that contained multiple trophic groups, hampering interpretation. Therefore, we ran an additional meta-regression on subgroup III to test hypothesis (1). Subgroup III contained only data points on herbivores (including
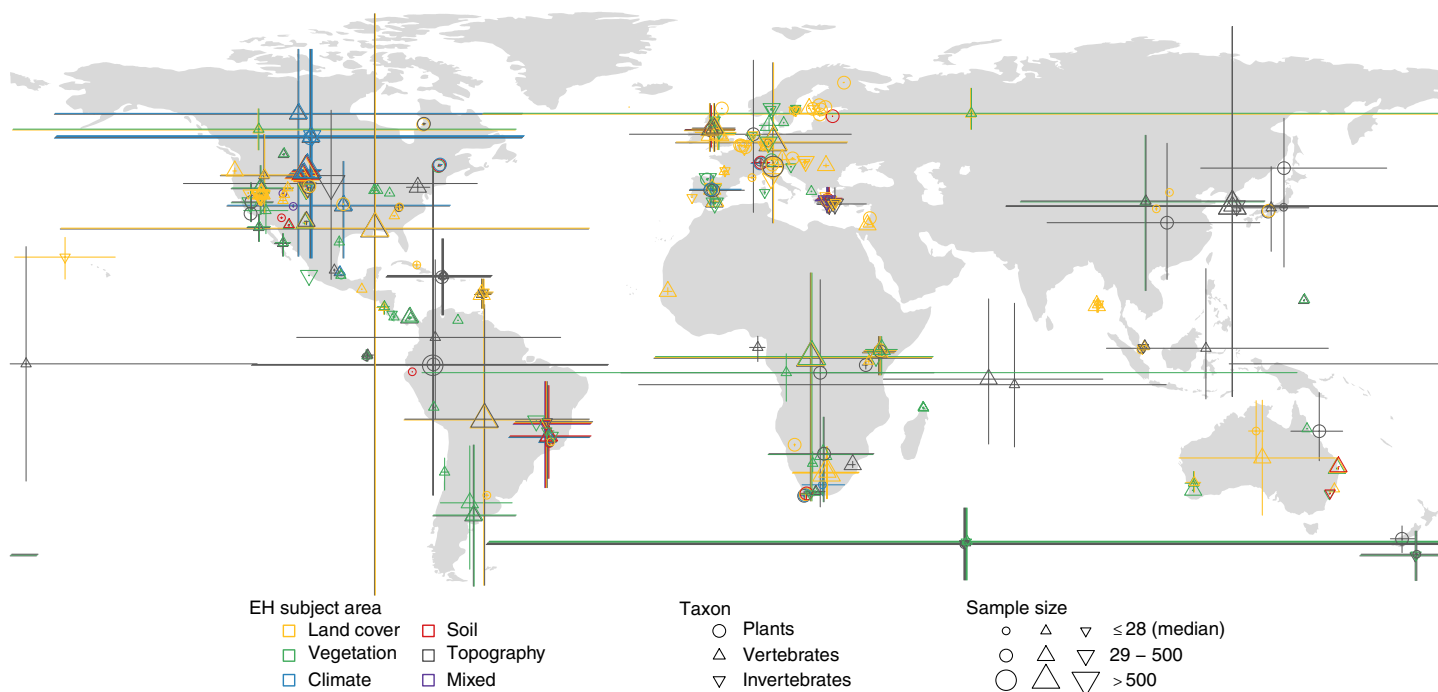
Figure 1 Locations of 192 studies contributing a total of 1148 data points to the meta-analysis of EH–richness relationships, distinguished by EH subject area (colour), taxonomic group (symbol) and sample size (symbol size). Symbols mark study location centroids and lines represent latitudinal and longitudinal extents of study locations; three data points with global extent are not shown. Overlapping symbols and lines are slightly offset for clarity.
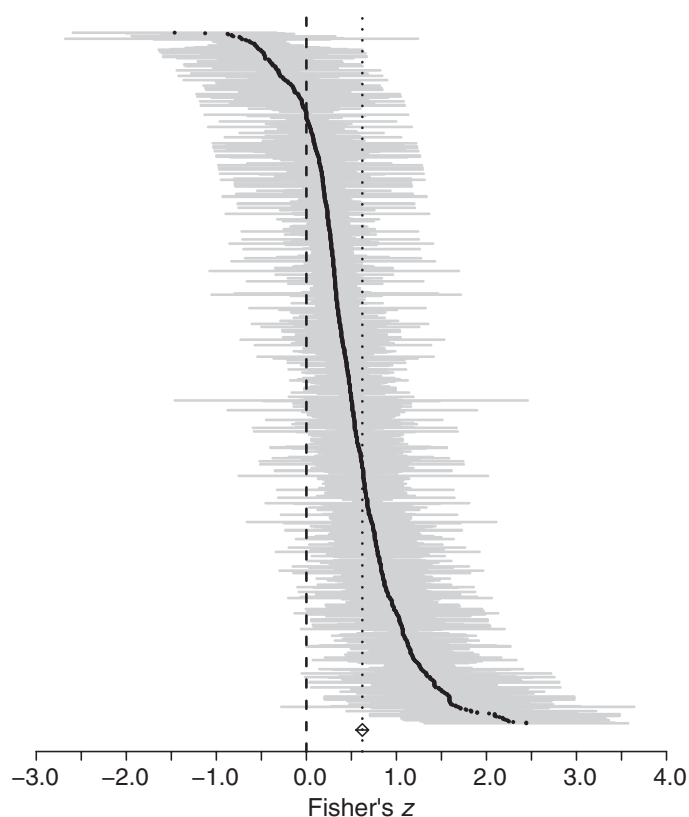
Figure 2 Forest plot showing 1148 effect size estimates of EH–richness relationships (black dots) with 95% confidence intervals (CI; grey lines). Black diamond and dotted line represent the overall weighted mean effect size estimate with 95% CI (diamond width); dashed line: zero effect.

frugivores) and was regressed against EH subject area as a fixed effect. Studies with climatic and soil EH were excluded due to low sample size. We split vegetation EH into vegetation structure and plant diversity, as we expected a stronger link of herbivores to plant diversity.

We used 99% CIs for subgroup meta-regressions to account for multiple testing (Gates 2002). We report R^2 values to indicate the proportion of variability explained by covariates; negative R^2 are truncated to zero (López-López *et al.* 2014). All statistical analyses were conducted in R v.3.0.1 (R Core Team 2013) using functions based on Hedges *et al.* (2010).

Publication bias

Publication bias arising from the preferential publication of statistically significant, positive and strong effects may impair meta-analytic conclusions (Møller & Jennions 2001). To test whether our results were affected by publication bias, we used funnel plots and Egger's regression test, by including standard error as a covariate in meta-regressions of the complete data set, equal-area studies only and subgroups I–III (Egger *et al.* 1997; Peters *et al.* 2008; Viechtbauer 2010). In case of funnel plot asymmetry, we ran additional regression tests using residuals of mixed-effects models to test for publication bias after controlling for heterogeneity (Egger *et al.* 1997; Nakagawa & Santos 2012). In addition, we calculated Rosenberg's fail-safe

number N for the complete data set as an indication of how many studies averaging null results would need to be added to render the overall mean effect size estimate non-significant (Rosenberg 2005; Jennions *et al.* 2013). We estimated N using study-level mean effect size estimates based on a fixed-effects model with the R package *metafor* (Viechtbauer 2010).

RESULTS

We compiled 1148 data points from 192 studies (Appendices S4 and S5). These included 190 scientific articles published in 71 journals between 1964 and 2011, one conference contribution and one thesis. The study areas covered all continents and biogeographic realms except Antarctica, with a strong bias towards the Palearctic (80 studies; Fig. 1, Appendix S6; note that one study may contain multiple study locations, taxa, spatial scales, or EH measures). Studies involved both mainland (142 studies) and island systems (52) and most often covered multiple habitat types (91) or focused on forest systems (57). Temperate forests (46 studies) and Mediterranean forests (24) were best represented, whereas studies from taiga (4), montane grassland (2) and tundra (1) biomes were scarce. Invertebrates (56 studies) were relatively underrepresented compared to vertebrates (85) and plants (67). Spatial grain ranged from 1 m² plots to 5° grid cells to provinces or islands of more than 10^{11} km²; spatial extent ranged from 10 km² to global. Most studies analysed EH in land cover (92 studies), topography (74) and vegetation (68), while few studies considered climatic (11) or soil EH (16; see Appendix S6 for more details).

Among the 1148 data points, 1012 showed positive and 134 showed negative EH–richness relationships, 758 and 59 of which, respectively, were statistically significant at $\alpha = 0.05$. Two outcomes were reported as correlations of 0.00. Effect size estimates varied between −1.46 and 2.44, but the overall weighted mean effect size estimate was significantly positive with $z = 0.63$ (95% CI $\pm$ 0.07; Fig. 2). The weighted mean effect size estimate of equal-area studies only was also distinctly positive, but lower with $z = 0.47$ ($\pm$ 0.09).

Meta-regressions assessing the effects of biotic vs. abiotic EH, EH subject area and measure category were performed without intercept; model coefficients can thus be interpreted as average effect size estimates (between-study effects; Figs 3 and 4). Coefficients for biotic vs. abiotic EH were close to the overall weighted mean and did not differ significantly from each other (0.63 ± 0.10 vs. 0.60 ± 0.10; Fig. 3). Coefficients for all five EH subject areas were also significantly positive, ranging from 0.34 ($\pm$ 0.27) for climatic EH to 0.67 for topographic ($\pm$ 0.13) and vegetation EH ($\pm$ 0.17; soil: 0.43 ± 0.29; land cover EH: 0.61 ± 0.12; Fig. 3). Average effect size estimates for topographic and vegetation EH were significantly larger than that for climatic EH (topographic EH: $t = 2.04$, $P = 0.04$; vegetation: $t = 2.08$, $P = 0.04$). Land cover EH had a larger average effect size estimate than climatic EH, but this difference was not statistically significant ($t = 1.78$, $P = 0.08$). Subject area coefficients were not significantly different otherwise.

In the meta-regression with EH measure categories, average effect size estimates varied between 0.20 ($\pm$ 0.47) for patchiness and 1.35 ($\pm$ 0.81) for microtopography (Fig. 4). All
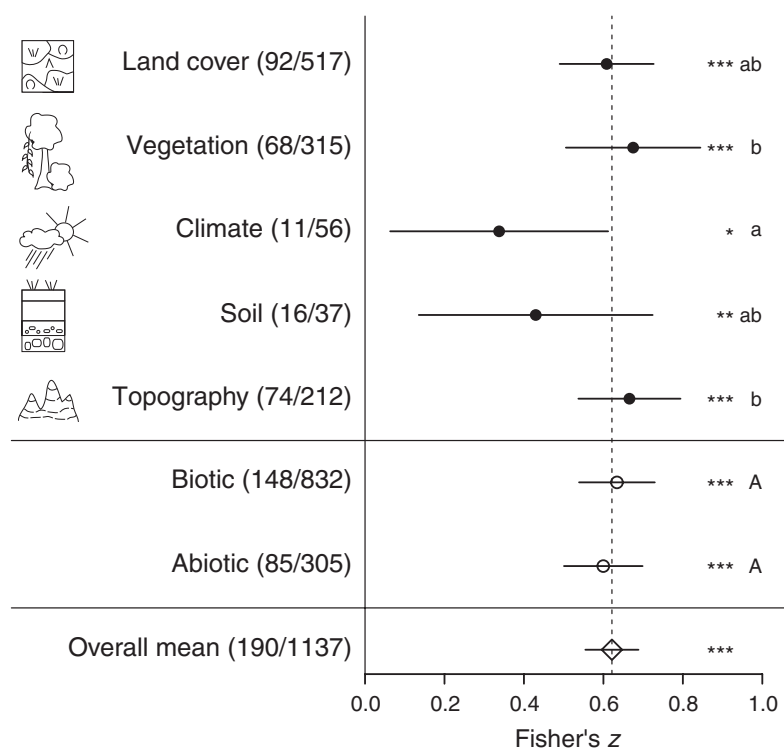
Figure 3 Mean effect size estimates for the five EH subject areas and for biotic vs. abiotic EH derived from two separate mixed-effects meta-regressions. Closed and open circles represent coefficients for EH subject areas and biotic vs. abiotic EH, respectively; lines show 95% confidence intervals (CI). Letters indicate significant differences among EH subject areas (lower case) and among biotic vs. abiotic EH (upper case). Diamond and dashed line represent the overall weighted mean effect with 95% CI; 11 data points mixing EH subject areas are excluded. Numbers in parentheses give the respective numbers of studies/data points; note that one study can include multiple EH subject areas and both biotic and abiotic EH. All coefficients are different from zero at significance levels: *** 0.001, ** 0.01, * 0.05.

coefficients except those for patchiness and soil variables were significantly positive. As in the results for overall mean effect size, coefficients for equal-area studies tended to be slightly smaller than coefficients for the complete data set (Fig. 4). Average effect size estimates for soil diversity and vegetation dimension were non-significant when investigating equal-area studies only.

We found stronger effects of covariates in multiple meta-regressions of subgroup I than of subgroup II. For subgroup I (considering only the EH measure categories elevation and land cover diversity), all covariates related to spatial scale were significantly associated with average effect size, whereas EH measure category showed no effect (model 1, Table 3a, Appendix S7). Studies that analysed equal-area units showed smaller effects on average than studies that did not keep area constant. Studies using larger spatial grains found stronger positive associations on average between EH and species richness. This was true both for between- and within-study effects. The opposite was true for spatial extent – larger extents were associated with smaller effect size estimates. These relationships all remained statistically significant when location- and taxon-related covariates were added (models 2 and 3). We found no influence of mean PET (model 2). Studies covering multiple habitat types found larger effect sizes on average than studies in forest systems. We found no significant difference between studies in non-forest systems and in forest systems. Taxonomic group did not influence average

effect size estimates, whether fine or broad taxonomic groups were included (model 3; Appendix S8). For subgroup II (considering only the EH measure categories vegetation complexity and plant diversity), we found no significant influence of any included covariates except spatial grain (models 1 and 2; Table 3b). As with subgroup I, studies conducted at larger spatial grains were, on average, associated with larger effect size estimates. However, when both location- and taxon-related covariates were included in model 3, this relationship became non-significant ($t = 1.83$, $P = 0.07$).

The meta-regression for subgroup III (herbivores only) revealed that studies analysing land cover or topographic EH had significantly smaller effect size estimates on average than studies analysing plant diversity as a measure of EH (Table 4). Effect size estimates of studies analysing plant diversity did not differ significantly from those of studies analysing vegetation structure, although the latter tended to be smaller.

Considering publication bias, almost one third of the included data points did not have statistically significant EH–richness relationships. Still, our study included a relatively high number of data points with large sample sizes and small standard errors (Fig. S1). Using regression tests, we detected funnel plot asymmetry for the complete data set and for subgroup I (Appendix S9). However, no asymmetry was found in funnel plots based on mixed-effects model residuals of subgroup I or on effect size estimates of equal-area studies only.
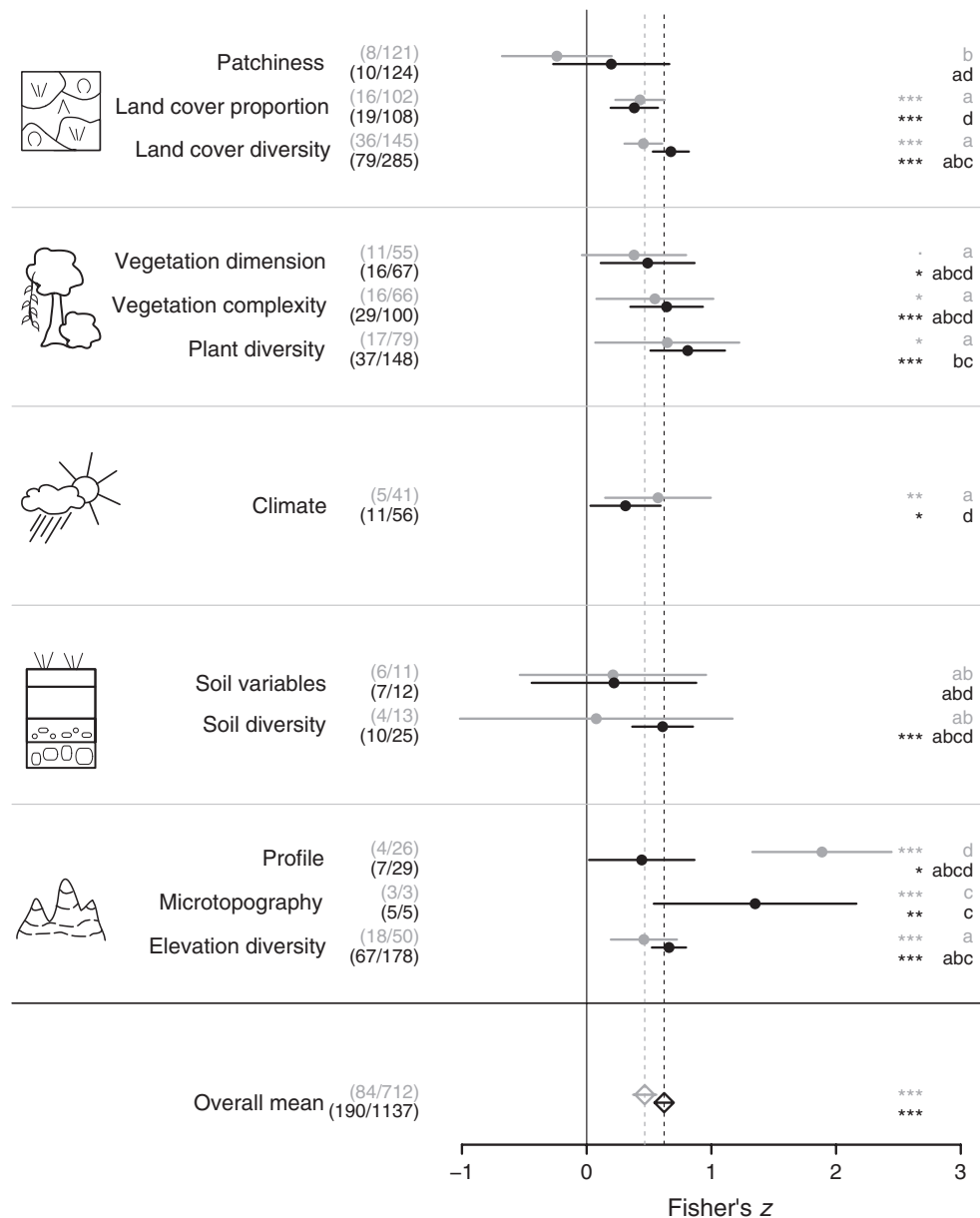
Figure 4 Mean effect size estimates of EH measure categories derived from mixed-effects meta-regressions considering either all or only equal-area studies. Black symbols refer to results for all studies, grey symbols to results for studies using equal-area units. Dots and lines represent coefficients with 95% confidence intervals (CI). Letters show significant differences among EH measure categories. Diamonds and dashed lines represent the overall weighted mean effects; 11 data points mixing EH measure categories are excluded. Numbers in parentheses give the respective numbers of studies/data points; note that one study can include multiple EH measure categories. Estimates for microtopography (equal area) not shown for clarity (8.3 ± 2.6). Significance levels indicating difference from zero: *** 0.001, ** 0.01, * 0.05.

Rosenberg's fail-safe number indicated that 211 470 studies with an average effect size of zero would need to be added to render the overall weighted mean (0.41 for a fixed-effects model of study-level mean effect size estimates) non-significant at α = 0.05.

DISCUSSION

Our meta-analysis of 1148 data points worldwide indicates that EH and species richness are on average positively related across taxa, regions and EH subject areas at landscape to

global extents. This positive relationship can be attributed to various mechanisms involved in the promotion of species coexistence, persistence and diversification. Several studies also reported negative EH–richness relationships or did not find any significant relationship at all, which was partly attributed to measures inadequate for the given study system, taxon or spatial scale (e.g. August 1983; Monadjem 1999; Marini *et al.* 2008). Some negative relationships were found between measures of vegetation structure and insect richness, which were ascribed to higher energy cost of movement in denser habitats or to the study taxa being adapted to more open

Table 3 Results of mixed-effects meta-regressions for subgroups representing different EH concepts: subgroup I: EH measure categories elevation diversity and land cover diversity (126/461 studies/data points); subgroup II: plant diversity and vegetation complexity (60/244 studies/data points)

	Model 1			Model 2			Model 3		
	b	SE	CI	b	SE	CI	b	SE	CI
(a) Subgroup I									
Intercept	0.77***	0.15	± 0.40	0.71***	0.21	± 0.54	0.73***	0.21	± 0.56
Equal area	−0.36***	0.08	± 0.21	−0.36***	0.08	± 0.21	−0.37***	0.08	± 0.22
Grain	0.05**	0.02	± 0.04	0.04*	0.02	± 0.05	0.04*	0.02	± 0.05
Grain.centred	0.08*	0.03	± 0.09	0.08*	0.03	± 0.09	0.08*	0.03	± 0.09
Extent	−0.07*	0.03	± 0.08	−0.11***	0.03	± 0.08	−0.11***	0.03	± 0.08
Elevation diversity	−0.04	0.11	± 0.28	−0.02	0.11	± 0.29	−0.04	0.12	± 0.30
Habitat mixed				0.31**	0.11	± 0.28	0.30**	0.11	± 0.28
Habitat non-forest				0.08	0.12	± 0.31	0.08	0.12	± 0.31
PET				0.00	0.00	± 0.00	0.00	0.00	± 0.00
Invertebrates							−0.08	0.12	± 0.32
Vertebrates							−0.03	0.08	± 0.22
(b) Subgroup II									
Intercept	0.70***	0.20	± 0.53	0.57*	0.27	± 0.72	0.54†	0.28	± 0.75
Equal area	−0.15	0.12	± 0.32	−0.13	0.12	± 0.33	−0.11	0.12	± 0.32
Grain	0.06*	0.03	± 0.07	0.07*	0.03	± 0.08	0.05†	0.03	± 0.08
Extent	−0.01	0.04	± 0.10	0.00	0.04	± 0.12	−0.02	0.04	± 0.12
Vegetation complexity	−0.24	0.15	± 0.39	−.19	0.17	± 0.45	−0.24	0.17	± 0.46
Habitat mixed				−0.08	0.16	± 0.43	−0.04	0.16	± 0.42
Habitat non-forest				0.13	0.21	± 0.56	0.17	0.22	± 0.58
Island				0.12	0.14	± 0.38	0.14	0.14	± 0.37
Vertebrates							0.25	0.16	± 0.43

Model 1 tests methodological covariates; models 2 and 3 test location- and taxon-related covariates while accounting for methodology and both methodology and study location respectively. Given are estimates of coefficients *b* for between-study effects (within-study effect for *grain.centred*, i.e. grain centred around the study-level mean), robust standard errors *SE*, and robust 99% confidence intervals *CI* to account for multiple testing. For details on covariates see Table 2; reference levels for categorical variables: EH measure category (a) *land cover diversity*, (b) *plant diversity*; habitat *forest*; taxon (a) *plants*, (b) *invertebrates*. R^2 of full model 3: subgroup I: 0.18; subgroup II: 0 (negative R^2, truncated to zero). Significance levels referring to *t*-test of difference from zero (intercept) or from reference level: ***0.001, **0.01, *0.05, †0.1.

Table 4 Results of mixed-effects meta-regression for subgroup III (herbivorous taxa only; covariate: EH subject area; 31/183 studies/data points)

Subgroup III	b	SE	CI
Intercept	1.07***	0.16	± 0.45
Land cover	−0.55**	0.19	± 0.53
Topography	−0.71**	0.22	± 0.60
Vegetation	−0.60	0.36	± 1.00

Given are estimates of coefficients *b* for between-study effects, robust standard errors *SE* and robust 99% confidence intervals *CI* to account for multiple testing. For details on covariates see Table 2; the reference level is *plant diversity*. Model R^2: 0.16. Significance levels referring to *t*-test of difference from zero (intercept) or from reference level: ***0.001, **0.01.

habitats (e.g. Humphrey *et al.* 1999; Lassau & Hochuli 2004). Furthermore, negative relationships have been found to occur predominantly at small spatial scales (Tamme *et al.* 2010). Appropriate EH measures are generally taxon dependent, often in interaction with spatial scale: body size and mobility, home range and habitat requirements determine whether a taxon perceives its environment as heterogeneous or is negatively affected by mobility constraints or fragmentation (Tews *et al.* 2004). Here, we could not test for effects of taxon-specific traits like body size or home range because studies often analysed groups as heterogeneous as mammals and vascular plants. Importantly, even though EH is highly context specific, overall mean effect sizes demonstrate the predominance

of positive EH–richness relationships across taxa and EH measures.

EH subject areas and measure categories

Overall, we found positive effects for all five EH subject areas, which makes sense considering that they can all be related to mechanisms promoting species coexistence, persistence and diversification. We found no differences in effects for biotic vs. abiotic EH, but comparing EH subject areas revealed more differentiated patterns: effects for vegetation and topographic EH were larger than for climatic EH. They were also larger than effects for soil EH, although not significantly so (Fig. 3). These larger effects make sense because vegetation EH, on one hand, is a more direct driver of species richness, particularly for herbivores, than climatic or soil EH. Vegetation EH is strongly associated with diversity of resources, shelter and roosting, breeding and oviposition sites, and with opportunities for divergent adaptation (e.g. Tews *et al.* 2004; Novotny *et al.* 2006; Kissling *et al.* 2007). By contrast, climatic and soil EH are likely to affect animal species richness indirectly via their effects on vegetation, although direct effects on speciation (Kisel *et al.* 2011), physiology and ecological preferences of species may also be important. Although the lower effects of climatic and soil EH are plausible given their indirect links to many organisms, we note that their coefficients are least precise due to lower sample size (Fig. 3). Topographic EH, on

the other hand, acts on richness in more diverse ways than climatic or soil EH: First, regions with high topographic EH have steep climatic and habitat gradients in relatively small areas, thereby promoting spatial turnover of species favouring different conditions (Kerr & Packer 1997; Kallimanis *et al.* 2008). Second, similar to climate and soil, topographic EH affects animal richness indirectly via its effects on vegetation EH. Finally, topographic EH promotes species persistence and diversification by providing refuges from adverse environmental conditions such as glaciation, and opportunities for diversification through geographic isolation (Rosenzweig 1995; Kallimanis *et al.* 2010; Särkinen *et al.* 2012). Therefore, highly heterogeneous tropical mountains may act as cradles and museums of biodiversity and are thus paramount in species richness and concentration of narrow endemics (Hughes & Eastwood 2006; Fjeldså *et al.* 2012).

In our model including EH measure categories, plant diversity, elevation diversity and land cover diversity showed comparatively large effects (Fig. 4). Measures included in these categories are among the most frequently used quantification methods and therefore had higher statistical power to detect an effect. However, it is also likely that these measures are more apt to quantify EH than e.g. patchiness or vegetation dimension. For instance, measures of plant diversity and vegetation complexity likely capture the requirements of many species better than measures of vegetation dimension. Although the taxonomic and functional composition and the physical structure of vegetation are closely linked, results on which component of vegetation EH is more important for herbivore diversity vary (e.g. Haddad *et al.* 2001; Brose 2003; De Araújo *et al.* 2013). While higher plant diversity should provide more diverse food resources and opportunities for specialisation, structurally complex vegetation is thought to contain more microhabitats and provide shelter and resting, breeding, oviposition and hibernation sites (Lawton 1983). Even within a single plant species, different herbivores often prefer different structures related to plant organs, vertical stratification, seasonal development or age classes (Lawton 1983). The significance of a particular measure also depends on the degree of specialisation of herbivores (De Araújo *et al.* 2013).

As with vegetation EH, different measures address different components of land cover EH: in contrast to measures of land cover diversity, which are often used as a proxy for spatial turnover of species, patchiness measures should be related more to fragmentation, which likely has more negative effects on species richness (Fahrig 2003). Although their higher effect sizes may seem plausible, measures of plant diversity, elevation diversity and land cover diversity were also the most frequently used measures at large spatial grains, suggesting that spatial grain may partly be responsible for the large effects of these measure categories found in our models. However, different measures inherently differ in their ability to predict species richness at different spatial grains (Böhning-Gaese 1997; Rahbek & Graves 2001).

Area constancy

As we expected, area constancy had an important role, as indicated by a significant negative effect of the covariate 'equal area' in meta-regressions of subgroup I (EH measure categories elevation and land cover diversity) and by the smaller mean effect size estimate for equal-area studies analysed alone (Table 3a, Fig. 4). Many EH measures scale positively with area, which makes disentangling the individual effects of EH and area difficult (Ricklefs & Lovette 1999; Triantis *et al.* 2003). For instance, count or range measures like number of habitat types, number of plant species and elevation range have, on average, larger values for larger areas. When area is not kept constant, effects of EH can therefore be confounded with direct effects of area on species immigration, extinction and speciation rates (compare MacArthur & Wilson 1967; Kisel *et al.* 2011). Controlling for the effect of area *per se*, the remaining effect of EH is likely to be smaller, as we found. However, we did not find a significant influence of equal area in models of subgroup II (EH measure categories vegetation complexity and plant diversity; Table 3b). Although we expected an effect of equal area on plant diversity, measures of vegetation complexity should be less affected by area. This may account for the overall non-significant effect we found, although we did find a negative effect when testing equal area in a single predictor model (-0.31 ± 0.36, $t = -2.25$, $P = 0.03$), suggesting confounding effects among covariates. Nevertheless, our findings provide strong empirical support for the idea that it is important to keep area constant in studies on EH–richness relationships (compare Whittaker *et al.* 2001). While methods to model multiplicative effects of EH and area have been proposed (Triantis *et al.* 2003), statistically controlling for area is problematic as collinearity may obscure the actual effect of EH (Whittaker *et al.* 2001). We therefore suggest that equal-area study units should be used as much as possible; at least for plot- and grid-based analyses this should be feasible.

Spatial grain and extent

We detected a positive effect of spatial grain in models of subgroups I and II (Table 3), also as expected. The fact that we found this effect both between and within studies (Table 3a) further stresses the importance of spatial grain, as confounding factors are less likely to be a problem in within- than between-study comparisons. There are multiple possible reasons for positive grain effects: First, larger units on average encompass more variability in EH, making stronger EH–richness relationships more likely (van Rensburg *et al.* 2002). Second, species turnover and allopatric speciation should become more important at larger spatial scales. Third, negative EH–richness relationships have been found mostly at small spatial scales, where (micro)fragmentation effects that increase the risk of species extinctions through isolation and habitat loss may be stronger (Tamme *et al.* 2010; Laanisto *et al.* 2013). Moreover, small-scale heterogeneity has been suggested to promote the dominance of a few species well adapted to heterogeneous conditions, thereby lowering overall species diversity (Gazol *et al.* 2013). Interestingly, previous studies have found indications of an opposite trend as well, i.e. of a negative effect of spatial grain on EH–richness relationships (Smith & Lundholm 2012). This may be due to a decline in variation between units occurring when more variation is included

within units (Wiens 1989). However, this decline depends strongly on the scale at which environmental variables are measured and vary, and on the distribution and spatial auto-correlation of variable values in an area (Siefert *et al.* 2012; Smith & Lundholm 2012).

It has also been argued that effect sizes measured at a particular spatial scale and comparative diversity analyses across study systems in general are affected by the size of the species pool (Chase & Knight 2013). Although we cannot rule out that some of the species richness data analysed in individual studies are biased in this way, sensitivity analyses suggest that our overall conclusions regarding the importance of EH are robust. To this end, we ran intercept-only models for two subsets that should be least affected by differences in species pool size and sampling scale: data points based on species lists or distribution maps and data points including only the largest spatial grain quartile. We detected no major differences between weighted mean effect size estimates of the subsets (0.68 ± 0.09 and 0.69 ± 0.11 respectively) and the complete data set (0.63 ± 0.07).

We found a negative effect of spatial extent in models of subgroup I (Table 3a), which is in line with expectations of EH being more important at intermediate extents and climate being the strongest driver of species diversity at large extents (Sarr *et al.* 2005; Field *et al.* 2009). This can partly be explained by the fact that climatic variables usually vary across relatively broad spatial scales (Siefert *et al.* 2012). Furthermore, some EH might average out with increasing spatial extent (Kolasa & Rollo 1991). The importance of EH is thought to be linked to spatial extent through a hump-shaped relationship (Sarr *et al.* 2005), but inclusion of a quadratic term in our meta-regressions did not support this idea. Supplementing our database by small-scale studies should give further insights into this topic. We note, however, that many studies did not provide spatial extent and that some of our estimations were inevitably imprecise. We therefore urge authors to provide clear and detailed information on study characteristics (also see Hillebrand & Gurevitch 2013).

Study location

We expected a positive effect of ambient energy, measured as mean PET, as previous studies have found topographic EH to be much more important for mammal and plant species richness in high than in low energy regions (Kerr & Packer 1997; Kreft & Jetz 2007). The surprising lack of a PET effect in our models may partly have been caused by imprecise spatial extents and therefore imprecise PET values in our data set. Also, studies were not evenly distributed spatially across the full range of PET values. A further explanation for our negative findings may be the fact that many study areas were large and thus contained a high variability in PET, which was evened out using mean PET in meta-regressions. To test this, we ran an additional analysis on data points with relatively small spatial extents only, using the first quartile of either the absolute study extent or the latitudinal extent. In both cases, we still did not find a significant effect of PET, which suggests that PET may not be universally related to the strength of EH–richness relationships. However, we suggest that the inter-

action between energy availability and EH should be considered in future studies. In addition to the effect of physiological constraints, dispersal barriers constituted by topographic EH are likely to be more effective in high-energy regions, where taxa are usually adapted to a smaller range of climatic conditions than taxa in seasonal temperate zones (Janzen 1967). Also, diversification rates are assumed to be higher in high-energy regions (Kisel *et al.* 2011).

Models of subgroup I suggested a stronger effect of EH in regions with multiple habitat types than in pure forest systems (Table 3a). Partly, this may be an artefact because EH measured e.g. as the number of habitat types or elevation range should, on average, be larger for areas covering multiple habitat types. We did not find this effect for subgroup II (Table 3b), which indicates that vegetation EH should be less dependent on habitat type. This might be expected because, although plant diversity may also tend to be higher in regions with multiple habitat types, measures of vegetation complexity do not necessarily increase with the addition of habitat types. Although the difference was not statistically significant, effect size estimates for non-forest systems tended to be larger than those for forest systems. This makes sense because key structural elements have been found to be particularly important in non-forest systems such as agricultural fields or grasslands (Tews *et al.* 2004; Joseph *et al.* 2011).

Taxonomic and functional groups

We did not detect significant differences among taxa (Table 3 and Appendix S8), suggesting that EH is a universal driver of species richness across taxonomic groups. The surprising similarity in correlates of plant and animal species richness has been pointed out before (Field *et al.* 2009).

Analysis of subgroup III confirmed our hypothesis that vegetation EH is more important for herbivore richness than climatic or topographic EH (Table 4). This is likely due to the close association of plants and herbivores and the expected more direct effects of vegetation EH compared to abiotic EH. However, this relationship is again scale dependent and may get weaker at larger spatial scales (Hawkins & Porter 2003; Field *et al.* 2009). Also, while our data set did not allow for a more detailed analysis, differentiating between trophic groups or specialist and generalist species in future studies or in focused reanalysis of existing data sets may reveal an even higher importance of plant diversity for specialist species richness (Kissling *et al.* 2007).

Limitations

Although we aimed to examine a representative subset of the literature, we could only consider simple linear relationships between EH and species richness. The relationship, however, is not necessarily linear: a hump-shaped relationship has been proposed to occur due to an area–heterogeneity trade-off, i.e. a reduction in suitable area available to a particular species associated with increasing EH, which may increase the risk of stochastic extinctions (Kadmon & Allouche 2007). The validity of the area–heterogeneity trade-off hypothesis has been questioned (Hortal *et al.* 2009, 2013;

Carnicer *et al.* 2013) and was also generally not corroborated by our data set. In fact, hump-shaped or other non-linear EH effects were rarely addressed in the studies that formed our data set, although some relevant studies may have been excluded due to our statistical inclusion criteria. Some studies that did test higher order terms of EH measures found no improvement over linear models or detected saturating or s-shaped, but no decreasing relationships (e.g. Marini *et al.* 2008, 2011). Only a few studies found quadratic or hump-shaped relationships between richness of plants, birds or butterflies and heterogeneity in productivity or land cover types, which were partly attributed to an interaction with productivity levels (Seto *et al.* 2004; Haberl *et al.* 2005; Parviainen *et al.* 2010). The occurrence of quadratic relationships in these studies depended on spatial scale and study taxon, indicating an even higher complexity of EH–richness relationships. The shape of the relationship also depends on the chosen EH measure. For instance, lumbricid species richness was found to be linked to the percentage of forest cover by a hump-shaped relationship, whereas it was positively linked to the number of habitat types, which probably increased with decreasing forest cover (Vanbergen *et al.* 2007). Overall, authors who found hump-shaped or negative EH–richness relationships often related their findings to an inadequate quantification of relevant EH components and not to a potential area–heterogeneity trade-off. More frequent investigations of non-linear relationships in future studies or reanalyses of existing data sets should help resolving the question of the existence of and reasons behind hump-shaped EH–richness relationships.

Another limitation of our analysis is that correlations, used here as measures of effect size, do not automatically imply causal relationships. For instance, positive correlations between vegetation EH and animal richness may result from a dependence of both taxa on the same environmental variables or on different but spatially covariant variables (Kissling *et al.* 2007). Moreover, mixed-effects meta-regressions are inherently observational and thus do not signify causality either (Viechtbauer 2007): effect size estimates may be causally linked to other study characteristics that covary with the study characteristic of interest, thus leading to confounded conclusions. However, results from both experimental and simulation studies confirm our predictions and findings (e.g. Palmer 1992; Vivian-Smith 1997; Siemann *et al.* 1998; Tamme *et al.* 2010; Smith & Lundholm 2012). In addition, for spatial grain, RVE allowed us to corroborate our conclusions through modelling of within-study effects. A higher amount of within-study comparisons among taxa, EH measures, spatial scales and habitat types as well as large-scale collaborative and standardised future studies should provide further insights into the determinants of variability in EH–richness relationships (compare Borer *et al.* 2014).

Publication bias

We detected some taxonomic and geographical bias in the EH–species richness literature, but the broad scope of our analysis and our use of random-effects models allows for reasonable generalisations. Furthermore, we consider our conclusions robust to publication bias: First, in cases where we detected

funnel plot asymmetry, no indication of asymmetry remained when we considered equal-area studies only or residuals of mixed-effects models. This implies that asymmetry was caused by heterogeneity in the data rather than by publication bias, and that the heterogeneity was partly accounted for by the covariates (Nakagawa & Santos 2012). Second, although based on a fixed-effects model of study-level means and therefore not directly comparable to the models in our analysis, the large fail-safe number of 211 470 implies robustness of our results. Third, publication bias is expected to be less problematic in biological studies, which often report tests of multiple hypotheses and therefore often contain both significant and non-significant results (Jennions *et al.* 2013). This lines up with the relatively high number of non-significant data points in our analysis as well as the fact that most studies investigated multiple environmental variables. Moreover, we calculated some effect size estimates ourselves that were thus not subject to publication bias.

CONCLUSIONS

Our extensive meta-analysis for the first time provides strong quantitative support for the generality of positive EH–richness relationships from landscape to global extents across a wide range of taxa and regions worldwide. While effects of all EH subject areas were positive, more studies investigating effects of climatic and soil EH on species richness are needed to confirm or reject their lower effects on richness as found here. We detected a pervasive influence of spatial scale on EH–richness relationships: First, our study highlights the importance of keeping area constant in analyses of EH. Second, the positive effect of spatial grain supports previous findings that negative EH–richness relationships are more likely to occur at small spatial grains.

We call for more future empirical studies and syntheses focusing on non-linear effects to provide more detailed insights into the actual shape of the association and on the validity and generality of the area–heterogeneity trade-off hypothesis. Furthermore, we see a need for distributed, standardised collaborative studies across study systems as well as focused reanalyses of existing data sets to further differentiate the effects of EH across taxa, regions and spatial scales, and when using different EH measures. Despite an overall positive EH–richness relationship, much variability in effect sizes remains to be explained, and modelling of within-study effects and more data sets with more combinations of covariates are needed for more detailed understanding. Finally, to increase the pool of results that can be used for synthesis, we urge authors to provide clear and detailed information on their methodology and study characteristics, such as study area and spatial scale, sample size and data sources, and above all to include comprehensive statistical information, including test statistics for non-significant relationships.

AUTHORSHIP

HK conceived the idea; AS and HK designed the study; AS collected data; AS and KG performed the analysis; AS wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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