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thesis abstract

Environmental heterogeneity–species richness relationships from a global perspective

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Abstract. Spatial environmental heterogeneity (EH) is considered one of the most important factors promoting species richness, but no general consent about the EH–richness relationship exists so far. This is because research methods and study settings vary widely, and because non-significant and negative associations have also been reported. My thesis provides a comprehensive review of the different measurements and terminologies of EH used in the literature, and presents strong quantitative evidence of a generally positive relationship between biotic and abiotic EH and species richness of terrestrial plants and animals from landscape to global extents. In a meta-analysis and a subsequent case study comparing multiple EH measures and their association with mammal species richness worldwide, I furthermore reveal that the outcome of EH–richness studies depends strongly on study design, including both the EH measure chosen and spatial scale. My research contributes to a better understanding of the EH–richness relationship, while identifying future research needs.

Keywords. habitat diversity, heterogeneity measures, meta-regression, spatial grain, species diversity, terminology, topography, vegetation structure

Introduction and Methods

Spatial environmental heterogeneity (EH) has fascinated researchers from ecology, biogeography, conservation biology, and evolutionary biology for decades, and is considered one of the most important factors determining species richness (Tews et al. 2004, Field et al. 2009). Early research revealed positive relationships between vegetation structure and bird and lizard species diversity (MacArthur and MacArthur 1961, Pianka 1967), and close positive associations between area, EH and species richness were also recognized long ago (Hamilton et al. 1963, Williams 1964). Since then, many different studies have investigated the effect of EH on species richness. However, in addition to positive EH–richness relationships, negative, hump-shaped and non-significant relationships have also been found (e.g. Tamme et al. 2010, Allouche et al. 2012). Therefore, even though ecological theory predicts a positive effect of EH on species richness (reviewed in Stein and Kreft 2014), the generality of positive EH–richness relationships in nature is still debated.

Positive relationships between EH and spe-

cies richness have been attributed to ecological, historical and evolutionary mechanisms. First, increased EH leads to an increase in diversity of resources, structural complexity and other environmental conditions, which should increase available niche space and thereby promote species' coexistence (Hutchinson 1959). Second, increasing EH is expected to enhance species' persistence through the provision of shelter and of refuges from long-lasting adverse environmental conditions, such as glaciations (e.g. Svenning and Skov 2007). Finally, EH should increase the probability of species diversification through isolation or adaptation to diverse environmental conditions (e.g. Hughes and Eastwood 2006). Negative and hump-shaped EH–richness relationships are mainly thought to result from unfavourable fragmentation effects (Tamme et al. 2010, Fahrig et al. 2011) and an area–heterogeneity trade-off, i.e. a reduction in the area of individual habitat types associated with increasing EH (Allouche et al. 2012, but see, e.g., Hortal et al. 2013). Considering this range of possible mechanisms and factors involved, it is unsurprising that the relationship be-

tween EH and species richness is difficult to quantify and comprehend.

The difficulty of understanding EH–richness relationships also arises from the considerable variability in taxa, ecosystems and spatial scales addressed in different studies, and the fact that EH is measured in numerous different ways. For instance, EH has been quantified with regard to vegetation structure, plant diversity, topographical complexity and habitat diversity, and with many different measures based on indices, ranges and other calculation methods. Moreover, the terminology regarding EH is diverse and discordant, making it difficult to comprehend exactly what is being studied by individual studies and whether different authors refer to the same concept. Thus, the variability in EH–richness research hampers attempts to find and compare studies and limits our understanding of the general EH–richness relationship.

The overall aims of my thesis (Stein 2014) were to examine the concept and role of EH within a broad, global framework, and to synthesise the current state of EH–richness research, including abiotic and biotic EH and a wide range of taxonomic groups. I thereby aimed to gain a more fundamental and general understanding of the EH–richness relationship. To this end, I conducted an extensive, systematic review of the EH–richness literature, covering observational studies that analysed the relationship between EH and species richness of terrestrial plants or animals at landscape to global extents. Based on 192 studies including 1148 data points, I first scrutinised the methodology and terminology used in EH–richness research (chapter 1; Stein and Kreft 2014). Specifically, I investigated how EH has been quantified and termed, and I classified the various EH measures by subject area, such as vegetation or topography, and calculation method, such as range or standard deviation. I used this classification, combined with information on study taxon, location, habitat type and spatial scale, to identify trends and gaps in research. Moreover, I reviewed the postulated mechanisms underlying positive EH–richness relationships and linked them to the EH subject areas and other study characteristics like

taxon and spatial scale. The coherent framework developed in this chapter then allowed me to conduct a meta-analysis to examine the strength and direction of EH–richness relationships across terrestrial study systems worldwide (chapter 2; Stein et al. 2014). In this study, I tested whether the relationship is positive overall and whether it differs between EH measures, study taxa, habitat types and spatial scales, using mixed-effects meta-regression. I used Fisher's *z* as a measure of effect size and applied robust variance estimation to allow the combination of multiple, dependent effect size estimates per study in a single analysis (Hedges et al. 2010).

Based on the insights from the literature review, I then studied how different EH measures relate to each other. To this end, I computed 51 EH measures for all land areas worldwide, using various environmental datasets and a range of calculation methods (chapter 3; Stein et al. 2015). I investigated the variability in EH measures using correlation and principal components analysis. Furthermore, I analysed how different measures vary in their relationship with species richness of terrestrial mammals (derived from IUCN 2013) using simultaneous autoregressive models. I compared single-predictor models (each with one EH measure) with multi-predictor models that additionally accounted for current climate, biogeographic region and human influence. I computed conditional inference trees (Hothorn et al. 2006) to examine whether model support depended more on the subject area or calculation method of EH measures. Based on the strong scale-dependence of EH–richness relationships found in chapter 2, I kept the area of study units constant and conducted the analyses across three different grain sizes, which are commonly used in macroecological analyses (12,364 km², 49,457 km², and 197,829 km²; approximately 110 km × 110 km, 220 km × 220 km, and 440 km × 440 km, respectively).

Results and discussion

My review is the first, to my knowledge, that systematically quantifies the terms for EH combined with the measures used and mechanisms dis-

cussed in the literature. I revealed how heterogeneous and ambiguous the quantification and terminology of EH have been in past research: I identified 165 different EH measures, with even more measure variants, related to biotic EH in land cover and vegetation, and abiotic EH in climate, soil and topography. These measures were denoted by more than 350 measure names; for instance, elevation range was also called altitude, altitudinal range, elevation variability, relief, and topography. I also detected more than 100 terms for EH, which were often used synonymously and rarely clearly defined. Even worse, opposing definitions exist, and there is no clear consensus about the meaning of terms in the literature. Despite the ambiguity, some trends emerged from the review: for instance, habitat diversity was the most common term used in the dataset, followed by habitat heterogeneity. Terms containing "diversity", "complexity" or "structure" were mostly associated with count or index measures, whereas terms containing "heterogeneity" mostly referred to range measures.

I detected a clear bias in the use of EH measures in the literature. The most frequent EH measure overall was elevation range (56 studies), followed by the number of plant species and the number of land cover types (31 studies each). In contrast, more than 100 measures occurred in only a single study each. At the spatial scales considered in my thesis, studies of climatic and soil EH were clearly underrepresented compared to land cover, vegetation and topographic EH (quantified by 11, 12, 54, 65, and 20 measures, respectively). Moreover, there was an overrepresentation of studies addressing land cover EH in the Palaearctic realm, and an underrepresentation of invertebrate studies compared to studies of vertebrates and plants. As the largest part of biodiversity is found in the tropics and in invertebrates, future research concentrating on these gaps should provide important insights into the generalisability of our current knowledge. Further, while many studies compared multiple EH measures, taxa or spatial scales, focused reanalyses of existing datasets and future comparative studies should deepen our understanding of taxon- and scale-dependent

effects of EH.

I detected multiple mechanisms that were used in the literature to explain positive effects of EH on species richness. The majority of studies referred to niche theory, i.e. more diverse resources and increased niche space allowing more species to coexist. These studies mostly investigated how vegetation EH affects animal richness. Studies addressing evolutionary mechanisms mostly related richness to topographic EH, assuming higher topographic EH to increase the probability of diversification through isolation and adaptation to diverse environmental conditions (Simpson 1964, Ruggiero and Hawkins 2008). The fact that different studies investigate different mechanisms and accordingly use different EH measures may be another explanation for conflicting conclusions regarding EH–richness relationships.

In the quantitative meta-analysis, I found that EH–richness relationships were significantly positive across taxa and EH subject areas. Vegetation and topographic EH were particularly strongly associated with species richness, whereas there was no significant difference between biotic and abiotic EH in their association with species richness. An important finding was that spatial grain, spatial extent and the use of equal-area study units clearly influenced the strength of EH–richness relationships, at least for the data subset including measures related to land cover types and elevation. Studies that did not keep area constant generally overestimated EH–richness relationships. This is because many EH measures scale positively with area, which *per se* promotes species richness through effects on maximum population sizes, immigration, extinction and speciation rates (MacArthur and Wilson 1967, Kisel et al. 2011). Studies conducted at larger spatial grains reported, on average, larger effect size estimates, which makes sense for multiple reasons. First, larger study units are likely to contain higher EH, promoting the detection of positive EH–richness relationships (van Rensburg et al. 2002). Second, positive effects of EH on species turnover and allopatric speciation are likely to be more important at larger spatial grains. Finally, negative EH–

richness relationships due to fragmentation effects seem to occur particularly at small grain sizes (Tamme et al. 2010, Laanisto et al. 2013). In contrast to spatial grain, studies conducted at larger extents found, on average, smaller effects. This is probably because at large spatial extents climate becomes the dominant determinant of species richness (Sarr et al. 2005, Field et al. 2009). In conclusion, it is essential to consider spatial scale in EH–richness studies, and comparisons across multiple spatial grains and extents should foster understanding. More importantly, researchers should keep the area of study units constant wherever possible; statistically controlling for area has the drawback that collinearity between EH and area may obscure the effect of EH (Whittaker et al. 2001).

In chapter 3, I found clear differences, but also similarities, among the 51 EH measures and their geographical patterns. Several EH measures were remarkably weakly correlated with each other, and particularly the coefficient of variation showed distinct differences from the other calculation methods. Other EH measures were highly correlated, which is not surprising considering the close associations between the underlying variables and subject areas. For instance, greater topographic EH generally entails more variation in (micro)climatic conditions and soil types, and more potentially isolated valleys and peaks, thereby promoting the turnover of land cover types and vegetation over relatively short distances (Körner 2000, Moeslund et al. 2013). Global maps revealed large differences among regions worldwide with regard to different EH measures: while tropical mountain regions had high topographic and climatic EH, Eurasia was characterised by high land cover and soil EH, whereas tropical South America, central Africa and south-eastern Asia featured high vegetation EH.

I found that measures of climatic and topographic EH, as well as those based on counts and ranges generally received greatest support in models of global terrestrial mammal species richness, once current climate, regional effects and human influence had been accounted for. Meas-

ures based on the coefficient of variation and Simpson index generally received lower support across all spatial grains studied, although these measures have received high support for other variables and taxa at smaller spatial scales (e.g. Fraser 1998, Kumar et al. 2006). Thus, generalisations to smaller spatial scales and other taxa, such as specialised habitat or trophic groups, should be made carefully because different patterns can be expected.

Conclusions

My research provides a comprehensive assessment of the measurement and terminology of EH in biotic and abiotic conditions and of EH–richness relationships across taxa at relatively broad spatial scales. The literature on EH–richness relationships is in urgent need of more consistent and transparent terminology, and I hope that my work will prove useful in this regard. Unambiguous terms and measure names, clear definitions and the avoidance of unnecessary synonyms should foster the understanding, comparison and synthesis of studies and thereby promote the advancement of the field. Applying novel meta-analytical techniques to the rich body of EH–richness studies, I was furthermore able to provide the first quantitative support for the generality of positive EH–richness relationships across EH subject areas, habitat types, taxonomic groups and spatial scales. The considerable impact of spatial grain, spatial extent and area constancy on study outcomes revealed by the meta-analysis demands that these methodological aspects be considered explicitly in future EH–richness studies.

The findings from all chapters of my thesis agree in that the influence of EH on species richness is a complex and context-dependent topic, and that quantification methods greatly influence study outcomes. While some of the most common EH measures received high model support in chapter 3, many other measures have been developed and used (compare e.g. chapter 1; McGarigal and Marks 1995, McElhinny et al. 2005, Bouchet et al. 2014), and different measures are most appropriate for different study systems. EH measures should be chosen according to the specific

hypothesized mechanism, taxon, ecosystem and spatial scale of interest. Overall, the use of context-specific, functionally meaningful measures in addition to easily available proxies, and careful consideration of underlying processes, should help us not only quantify, but also truly understand EH–richness relationships. Because it is difficult to predict *a priori* which measure or spatial scale is most appropriate, comparative studies across EH subject areas, selected calculation methods and spatial scales, as well as focused reanalysis of already existing datasets, should allow more detailed insights into the EH–richness relationship. Mechanistic interpretations were relatively rare in the reviewed literature, echoing previous reports of missing links between theories and data in the ecological literature in general (Scheiner 2013). Considering the great variety in mechanisms underlying EH–richness relationships, it is not surprising that the strengths of reported associations vary. Stronger involvement of theory and processes in EH–species richness studies should promote greater understanding and generalisation.

Despite the advancements made in the field of EH–richness relationships with my thesis, many gaps in our understanding still remain. Scrutinising effects of EH on separate functional groups and across more evenly distributed habitat types and regions worldwide (including more studies in tropical and arid regions) should provide further insights in the future. Also, more studies are needed with more complex statistical approaches, including the consideration of non-linearity, to fully understand EH–richness relationships. But with the new, solid foundation for further research provided by my thesis, it will hopefully not be long before the question of how EH affects species richness is thoroughly understood.

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