

Terminology and quantification of environmental heterogeneity in species-richness research

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ABSTRACT

Spatial environmental heterogeneity (EH) is an important driver of species diversity, and its influence on species richness has been analysed for numerous taxa, in diverse ecological settings, and over a large range of spatial scales. The variety and ambiguity of concepts and terminology, however, have hampered comparisons among studies. Based on a systematic literature survey of 192 studies including 1148 data points, we provide an overview of terms and measures related to EH, and the mechanisms that relate EH to species richness of plants and animals in terrestrial systems. We identify 165 different measures used to quantify EH, referred to by more than 350 measure names. We classify these measures according to their calculation method and subject area, finding that most studies have analysed heterogeneity in land cover, topography, and vegetation, whereas comparatively few studies have focused on climatic or soil EH. Overall, elevation range emerged as the most frequent measure in our dataset. We find that there is no consensus in the literature about terms (such as ‘habitat diversity’ or ‘habitat complexity’), their meanings and associated quantification methods. More than 100 different terms have been used to denote EH, with largely imprecise delimitations. We reveal trends in use of terms and quantification with respect to spatial scales, study taxa, and locations. Finally, we discuss mechanisms involved in EH–richness relationships, differentiating between effects on species coexistence, persistence, and diversification. This review aims at guiding researchers in their selection of heterogeneity measures. At the same time, it shows the need for precise terminology and avoidance of ambiguous synonyms to enhance understanding and foster among-study comparisons and synthesis.

Key words: cross-taxon comparison, global study, habitat diversity, habitat structure, heterogeneity measures, landscape complexity, structural complexity, synonymy.

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I. INTRODUCTION

(1) Background: environmental heterogeneity in biodiversity research

The relationship between spatial environmental heterogeneity and species diversity is a central topic in ecology, evolution, and biogeography. Seminal research on birds (MacArthur & MacArthur, 1961), lizards (Pianka, 1967), and plants (Hamilton *et al.*, 1963; Johnson & Simberloff, 1974) already encompassed various aspects of heterogeneity and structure in the environment. For instance, MacArthur & MacArthur (1961) highlighted the importance of vegetation structure for local bird species diversity, and Williams (1964) pointed out that an increase in study area usually entails an increase in variety of environmental conditions and habitat types. Since then, numerous studies have investigated the influence of environmental heterogeneity on many different taxonomic groups in various aquatic and terrestrial systems.

The overarching ecological hypothesis is that spatial heterogeneity in abiotic or biotic conditions increases the available niche space and therefore allows more species to coexist (Currie, 1991; Tews *et al.*, 2004). At larger spatio-temporal scales, environmental heterogeneity may affect diversification and extinction rates through isolation, specialization, and provision of refugia where populations persist during periods of climate change (Pianka, 1966; Cowling & Lombard, 2002; Durães & Loiselle, 2004; Kallimanis *et al.*, 2010; Sandel *et al.*, 2011). Although negative relationships between environmental heterogeneity and species diversity have also been reported (Tamme *et al.*, 2010; Gazol *et al.*, 2013; Laanisto *et al.*, 2013), a recent global meta-analysis found the overall relationship to be positive across taxa and spatial scales, as predicted by ecological theory (Stein, Gerstner & Kreft, 2014).

Previous reviews of the relationship between environmental heterogeneity and species diversity often focused only on one selected aspect of heterogeneity and a restricted taxonomic group. For instance, Tews *et al.* (2004) studied the effect of vegetation heterogeneity on animal diversity. Lundholm (2009) and Tamme *et al.* (2010) in turn reviewed the relationship between abiotic heterogeneity and plant diversity at relatively small spatial scales. Here, we consider spatial heterogeneity in both abiotic and biotic environmental conditions, including studies across taxonomic groups and a range of spatial scales.

(2) Concepts and terminology

The ecological literature contains an astonishing number of different terms for environmental heterogeneity, with often undefined or even conflicting underlying concepts. Some authors have distinguished heterogeneity as the horizontal component of habitat variation from complexity as the vertical component (August, 1983; Grelle, 2003). Kolasa & Rollo (1991) argued against an explicit distinction of these two dimensions because heterogeneity can have more than two dimensions in space or time. These authors, however, differentiated between continuous and patchy heterogeneity, thus contrasting gradual from discrete changes in environmental conditions. Others have discriminated variability ('different values of a variable of one kind') from heterogeneity ('composition of parts of different kinds') (compare Kolasa & Rollo, 1991; Wagner, Wildi & Ewald, 2000). Ettema & Wardle (2002) defined variability as a general term for spatial changes and heterogeneity or patchiness as terms for changes involving spatial structure and aggregation. Nilsson, Bengtsson & Ås (1988) considered habitat heterogeneity to be one aspect of habitat variability, and habitat diversity to be a second aspect. By contrast, Li & Reynolds (1995) defined variability and complexity as components of heterogeneity, referring to quantitative *versus* qualitative descriptors of ecological properties. Several authors have emphasized a difference between variability within and between habitat types: while habitat diversity has often referred to the number of habitat types in a given area (i.e. between-habitat variability), habitat complexity or habitat heterogeneity have been used frequently to describe within-habitat variability (August, 1983; Nilsson *et al.*, 1988; Heaney, 2001; Hortal *et al.*, 2009; Table 1). These opposing concepts can be confusing, even more so because many authors have used terms such as (environmental/habitat) heterogeneity, diversity, complexity, structure, or variability synonymously or without a precise definition and delimitation (e.g. Johnson, 1975; Perfecto & Snelling, 1995; Durães & Loiselle, 2004; Ackerman, Trejo-Torres & Crespo-Chuy, 2007). It can therefore be difficult to determine whether terms used in different studies refer to the same concept or not (McCoy & Bell, 1991). Inconsistent terminology hampers the detection, understanding, comparison, and synthesis of studies. Literature searches necessarily remain incomplete: for instance, Tews *et al.* (2004) included 'habitat complexity' in their keyword search, whereas studies using the term 'complexity of habitat'

Table 1. Glossary of terms related to spatial environmental heterogeneity.

Environmental heterogeneity (EH)	Used here as an umbrella term for all kinds of spatial heterogeneity, complexity, diversity, structure, or variability in the environment. Although ‘habitat diversity’ is more common in the literature, we consider ‘environmental heterogeneity’ to be the most comprehensive term. First, ‘habitat diversity’ often refers to the diversity of different habitat types only. Second, ‘environmental’ can relate to all aspects of the environment, whereas ‘habitat’ has variable definitions (Triantis <i>et al.</i> , 2003).
EH subject areas	EH contains biotic and abiotic components that can be divided into five subject areas: land cover, vegetation, climate, soil, and topography.
Land cover EH	Heterogeneity between habitats, including composition and configuration. Most often quantified as the number or Shannon diversity index of land cover (or habitat/vegetation) types.
Vegetation EH	Incorporates vegetation structure (e.g. foliage height diversity) and plant diversity (e.g. the number of vascular plant species).
Climatic EH	Heterogeneity in micro- to macroclimatic conditions, most often quantified as precipitation range.
Soil EH	Mostly quantified as the number of soil types, but can also relate, e.g. to variability in soil pH, cation content or soil compaction.
Topographic EH	Incorporates microtopographic structure to large-scale relief. Most often quantified as elevation range, the most frequent EH measure overall.
Habitat complexity	Usually refers to vegetation EH, as does ‘habitat structure’ and ‘structural complexity’.
Habitat diversity	The most frequent term in the literature, most often related to the number of different land cover (or habitat/vegetation) types.
Habitat heterogeneity	The second most frequent term in the literature, which in contrast to ‘habitat diversity’ is thought by some authors to incorporate both within- and between-habitat variability (Nilsson <i>et al.</i> , 1988).
Landscape complexity	In contrast to ‘habitat complexity’ and ‘habitat structure’, ‘landscape complexity’ and ‘landscape structure’ usually refer to between-habitat heterogeneity, quantified as the Shannon diversity index of land cover types or percentage of forest area, for instance.

were missed. In addition to using variable terminology, studies have encompassed various quantification methods, taxonomic groups, geographic settings, and diverse study designs. This conceptual and methodological variability may obscure our understanding of the role and importance of environmental heterogeneity on species diversity.

(3) Aims of this review

Although the variety in quantification and the ambiguity in terminology of environmental heterogeneity are a recognized predicament, to our knowledge, no systematic overview of terms and quantification methods exists so far. To fill this gap, we systematically reviewed empirical studies on the relationship between spatial environmental heterogeneity and species richness of plants and animals in terrestrial systems. For reasons of clarity, we use the term ‘environmental heterogeneity’ *sensu lato* (from now on ‘EH’) as an umbrella term including all other related terms, meaning all aspects of spatial heterogeneity, complexity, diversity, structure, or variability in the environment (Table 1). Temporal heterogeneity has also received significant attention in the literature, but we do not treat it here, as it affects species richness through different mechanisms compared to spatial heterogeneity, related to stability and disturbance (Menge & Sutherland, 1976; Currie, 1991).

We distinguish between ‘terms’ used to signify EH in each study (e.g. ‘environmental complexity’ or ‘habitat diversity’) and ‘measures’ that were actually quantified as proxies of EH (Table 2). We aimed to reveal overarching trends in terms and measures across study systems and to review the different theories explaining heterogeneity–richness relationships. Compared with previous reviews, we concentrated on larger spatial scales and included studies on both animal and plant species richness.

EH has been measured over a wide range of spatial scales and in the context of diverse taxonomic groups that vary widely in traits like body size and ecological requirements. Unsurprisingly, highly diverse measures have been applied to each particular setting. With regard to the thematic focus of these measures, we distinguish between different ‘subject areas’, for instance EH related to topography or vegetation (Fig. 1). Furthermore, we refer to the methodological and mathematical approach employed for each measure as its ‘calculation method’ (see Table 2 for examples).

Specifically, we addressed the following questions: (i) which terms and measures of environmental heterogeneity have been used, and in which combinations? (ii) How can these measures be classified by methodology and subject area? (iii) Are there trends in the terminology and quantification of environmental heterogeneity regarding different concepts, methodological approaches, spatial scales, study locations or

Table 2. Common terms of environmental heterogeneity (EH) with exemplary measures used for quantification, the according calculation method and the subject area used in our framework (see text and Fig. 1). A given term of EH may be quantified by different measures in different studies or even within the same study.

Term	Measure	Calculation method	Subject area	Exemplary references
Environmental heterogeneity	CV of precipitation	CV	Climate	Durães & Loiselle (2004) and Fraser (1998)
	# soil types	Count	Soil	Durães & Loiselle (2004) and Johnson & Simberloff (1974)
Habitat diversity	# land cover types	Count	Land cover	Deshaye & Morisset (1988) and Kohn & Walsh (1994)
	Elevation range	Range	Topography	Ferrer-Castán & Vetaas (2005) and Finch, Blick & Schuldt (2008)
Habitat heterogeneity	SD of elevation	SD	Topography	Joly & Myers (2001) and Pereira, Oliveira-Filho & Lemos-Filho (2007)
	Elevation range	Range	Topography	Kerr & Packer (1997) and Kissling <i>et al.</i> (2008)
Landscape structure	% forest cover	Percentage	Land cover	Danell <i>et al.</i> (1996) and Ma (2008)
Structural complexity	Foliage height diversity	Index	Vegetation	Karr & Roth (1971) and Orians (1969)

Abbreviations: CV, coefficient of variation; #, number of; SD, standard deviation.

taxa? (iv) Which mechanisms have been proposed to explain positive EH–richness relationships and how are they linked to subject areas, spatial scales, taxa and habitat types?

II. REVIEW OF STUDIES ON EH–RICHNESS RELATIONSHIPS

(1) Literature search and data basis

The literature reviewed here was compiled in the framework of a meta-analysis investigating the strength of EH–richness relationships (Stein *et al.*, 2014). Our systematic literature survey included three different search modes: (1) a comprehensive keyword search in *ISI Web of Science* on the 19th April 2011, including all years and using combinations of different terms for EH (e.g. ‘habitat diversity’, ‘habitat heterogeneity’, ‘structural complexity’, ‘topograph* heterogeneity’) and “‘species diversity’ OR ‘species richness’ OR ‘species number’ OR ‘species density’” (see online supporting information Appendix S1 for details), (2) an inspection of the studies cited in several review articles (Ricklefs & Lovette, 1999; Tews *et al.*, 2004; Field *et al.*, 2009; Hortal *et al.*, 2009; Lundholm, 2009; Tamme *et al.*, 2010), and (3) a screening of the studies cited in the articles detected by search modes (1) and (2). Studies were selected according to a set of inclusion criteria (see Stein *et al.*, 2014 for details). In brief, the meta-analysis only included observational studies that quantified the relationship between EH and species numbers of plants or animals in terrestrial systems at landscape (> 10 km²) to global extents.

We recorded the terms used to indicate EH in each study and the according measures used to quantify EH. We also compiled information on the study taxon, location [biogeographic realm according to Olson *et al.*, 2001, geographic

coordinates, insularity, main habitat type (agricultural, forest and woodland, grassland, mixed, montane, or xeric)], and methodology (data source, such as fieldwork or literature data; data type, such as species lists or range maps; spatial scale). In addition, we recorded the mechanisms behind EH–richness relationships mentioned in each study and compiled bibliographic data (publication year and type, language, journal). If coordinates and spatial scale could not be obtained directly from the articles or authors, we used a geographical information system (ESRI, 2010) to estimate these variables. Spatial scale contains multiple components that are in some cases confounded or defined differently (Scheiner *et al.*, 2000; Lundholm, 2009; Whittaker, 2010). We recorded the spatial grain of each study as the area of the unit of analysis, which was equivalent to the spatial focus in almost all studies (compare Scheiner *et al.*, 2000; Scheiner & Jones, 2002). If the units of analysis varied in area, we used the mean area, or, when not available, the midrange, as spatial grain size. The area sizes of sample units of species richness data and EH data were only available in some of the studies. Spatial extent was recorded as the study area as given in the article or otherwise as the size of the area of a minimum convex hull encompassing all study sites.

We included 192 studies in our analysis (listed in online Appendix S2). Many studies analysed EH–richness relationships based on multiple study sites, spatial scales, taxa, or EH measures. We recorded this information as separate data points, leading to a total of 1148 data points in our database. The majority of studies employed multiple terms for EH, but we did not treat them as separate data points unless they explicitly referred to different measures. As a consequence of there being multiple data points per study, the percentages reported in the following sections frequently add up to more than 100%. For instance, in a hypothetical dataset

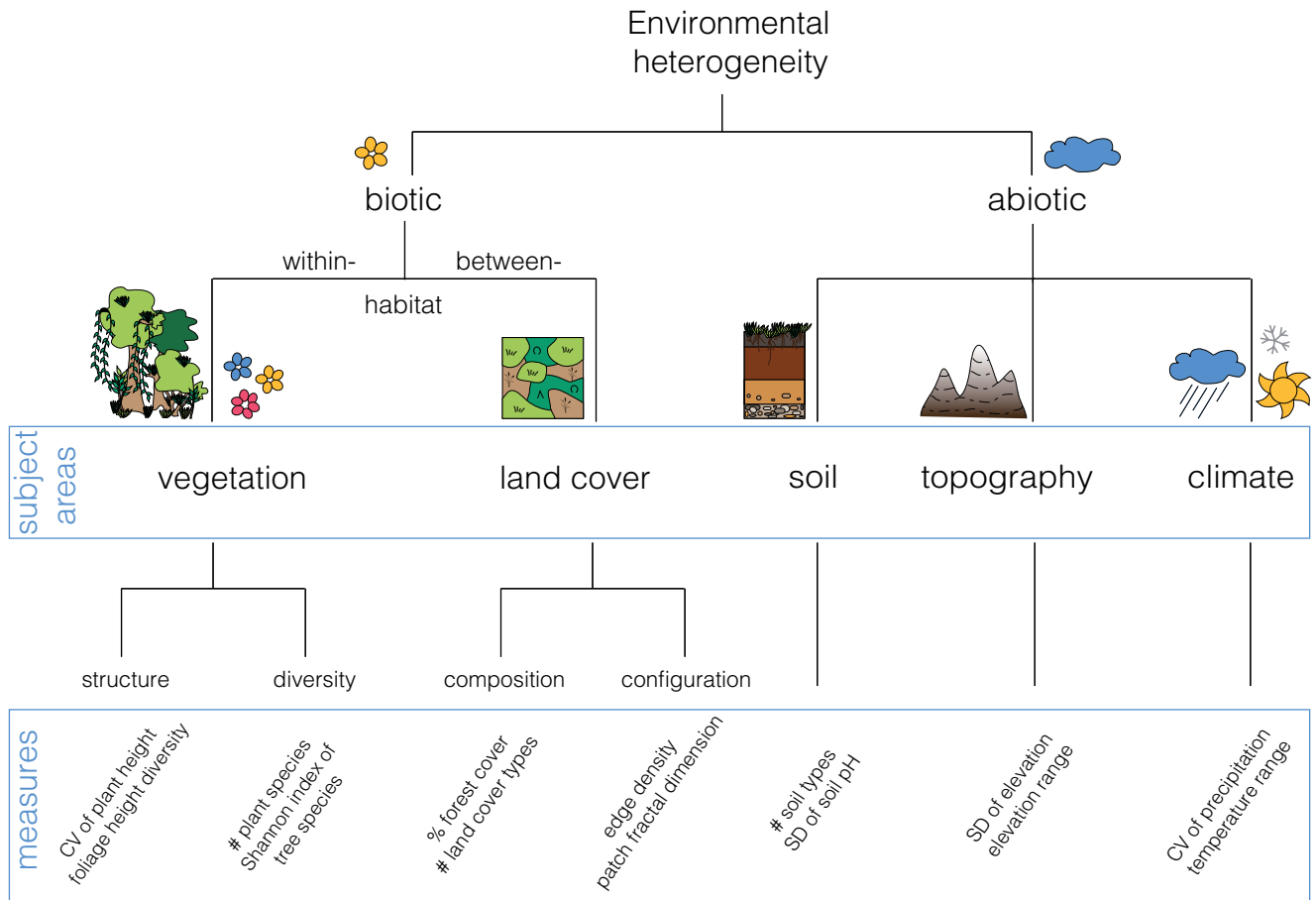


Fig. 1. Components and quantification of environmental heterogeneity (EH). EH can be differentiated into biotic and abiotic components, which are represented by five subject areas: vegetation (within-habitat component, i.e. vegetation structure and plant diversity), land cover (between-habitat component, composition and configuration), soil, topography, and climate. Note that biotic EH may incorporate heterogeneity in organisms other than plants, which is not included in this review (see text). At the bottom, exemplary measures are given for each subject area (for abbreviations see Table 2).

of two studies, one study might contain one data point on vertebrate species richness, the second study one data point on vertebrate richness and one on plant richness. Thus, 100% of the studies analyse vertebrate richness and 50% analyse plant richness, adding up to 150%. In the following, the reference for a particular percentage is always the population of studies that is currently being discussed. For instance, the percentage of studies analysing topographic EH may refer to all studies or to only a subset of studies that is currently discussed, such as studies including vertebrate richness.

The studies were published between 1964 and 2011 in 71 different journals; we also included one thesis and a conference contribution (see online Appendix S2). Approximately half of the studies were published in the last decade (Fig. 2, inset). The journals with the highest representation in our database were *Journal of Biogeography* (35 studies), *Biodiversity and Conservation* (15), *Ecology* (12), *Ecography* (9), and *Global Ecology and Biogeography* (8). Forty-six journals were represented by a single study each. Most articles were published in English, but we included one study each in French and in Spanish.

Clearly, our dataset does not cover the entire body of literature that exists on the relationship between EH and species diversity. Our literature survey, although extensive and following multiple search strategies, necessarily remains selective. Moreover, we had to exclude interesting studies that did not conform to the inclusion criteria (Stein *et al.*, 2014). Due to the wide scope and standardized approach of our literature search and study selection, however, we are confident that we have compiled a representative subset of the relevant literature.

(2) Subject areas

In contrast to previous reviews, we considered all kinds of spatial heterogeneity in environmental conditions. We detected five EH subject areas: studies have measured EH in vegetation, land cover, climate, soil, and topography (Table 1). These subject areas represent biotic as well as abiotic components of heterogeneity (Fig. 1).

EH–richness relationships are studied from small to large spatial scales. With regard to abiotic EH, this involves, for

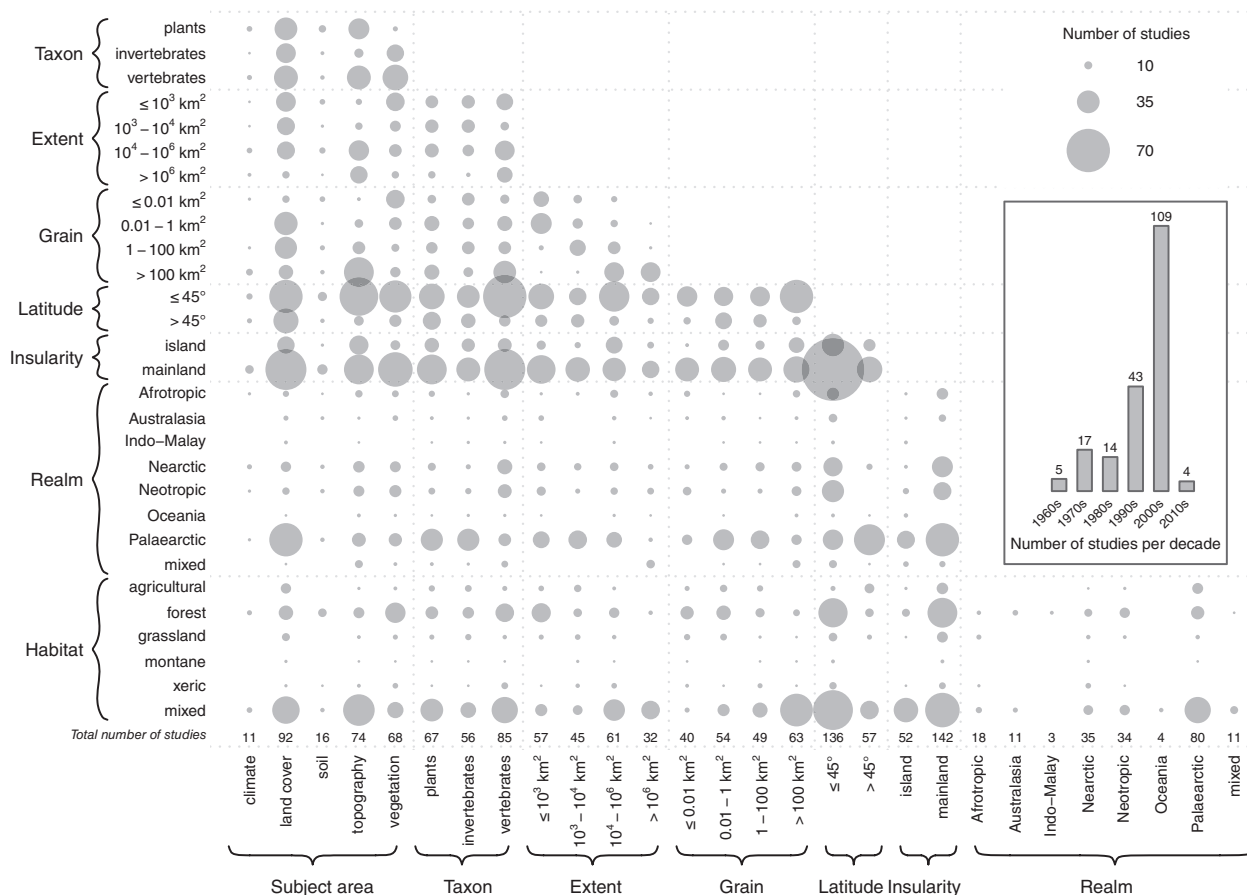


Fig. 2. Representation of subject areas of environmental heterogeneity (EH), taxonomic groups, spatial extent and grain, latitude (absolute latitude of centroids), insularity, biogeographic realms, and main habitat types in our dataset. Bubble size is proportional to the number of studies analysing each combination of variables and increases continuously; legend provides exemplary bubble sizes. The inset shows the number of published studies per decade; note that the last decade only includes studies published up to April 2011.

instance, micro- to macroclimatic conditions concerning energy or water budget, or microtopographic structural elements to large-scale topographic relief. The subject areas are often closely linked; changes in elevation, i.e. in topographic EH, entail changes in temperature, precipitation, wind and insolation, i.e. in climatic EH, for example.

Vegetation EH incorporates the physical structure of vegetation on one hand and its functional or taxonomic composition, i.e. plant diversity, on the other hand. These are closely linked because higher plant diversity often entails a more complex vegetation structure (Qian & Kissling, 2010). Vegetation EH can also be considered from small-scale structure – the architecture of single plants – to larger scale heterogeneity of a complete forest. Measures of vegetation EH refer to within-habitat EH as we define it. Even when covering multiple (micro)habitat types, these measures do not focus on separate patches of habitat but relate to the overarching structure or composition of the study site irrespective of the contained types of patches (e.g. foliage height diversity across multiple vegetation types in Panama: Karr & Roth, 1971). In some cases, measures of vegetation

EH refer to a vertical component of EH, for instance a measure of vegetation stratification (number of vegetation layers: Kati *et al.*, 2009; also see previous example). This would relate to ‘habitat complexity’ as defined by August (1983). Other vegetation measures, however, are not directly associated with vertical stratification but still represent the physical structure or composition of vegetation (e.g. density of trees: James & Wamer, 1982; coefficient of variation of trunk perimeters: Taboada *et al.*, 2010; or measures of plant diversity, e.g. number of plant species: Kitchener, 1982).

In contrast to vegetation EH, our definition of land cover EH explicitly considers multiple types or patches of habitat, i.e. between-habitat heterogeneity. EH in this context could be measured on a two-dimensional image of the study site (e.g. the diversity of habitat types derived from vegetation maps: Ricklefs & Lovette, 1999). Therefore, land cover EH is related to ‘heterogeneity’ or ‘horizontal variation’ *sensu* August (1983) or Grelle (2003). Still, land cover EH is closely related to vegetation, as it largely refers to habitat or land cover types that are often defined by vegetation structure and major vegetation classes (e.g. Ricklefs & Lovette, 1999;

van Rensburg, Chown & Gaston, 2002). Land cover EH incorporates the composition of cover types as well as their configuration, i.e. the spatial arrangement of elements (McGarigal & Marks, 1995; Turner, Gardner & O'Neill, 2001). Due to the predominance of composition measures in our dataset and because measures cannot always be assigned definitely to composition or configuration (McGarigal & Marks, 1995), we do not distinguish them here.

Biotic EH can relate also to other biotic components of the environment, including animals, fungi, or microbes. For instance, the diversity of prey species strongly influences the diversity of predator species (Sandom *et al.*, 2013). Cross-taxon richness relationships have been discussed in more detail elsewhere (e.g. Wolters, Bengtsson & Zaitsev, 2006; Vellend, 2008), and apart from vegetation EH they are usually described in terms unrelated to EH. Therefore, they barely emerged in our literature survey except those concerning vegetation EH, and we do not discuss them further (but see online Table S1).

A few composite measures exist that integrate multiple variables across different subject areas, e.g. summing up variables related to radiation, slope, rock fragments, and soil types (Harner & Harper, 1976; also see Brown & Freitas, 2000). Due to their rareness in our dataset, we focus on measures that can be assigned to a single subject area.

(3) Quantitative description of studies

(a) Study locations

The study regions covered all continents except Antarctica and both mainland and island systems. The most frequently studied biogeographic realm was the Palaearctic (41.7% of the studies; Fig. 2), followed by the Nearctic (18.2%) and the Neotropic (17.7%). Only 9.4% of studies focused on the Afrotropic realm. Eleven studies (5.7%) each were conducted in Australasia or included multiple biogeographic realms. The significant bias towards studies in temperate systems is further illustrated by the fact that three quarters of the studies were centred outside the tropics at latitudes above 23.5° and 29.7% above 45°. The majority of study areas covered mainland systems, 27.1% of the studies focused on islands. Given that islands cover only 5.3% of global land area (Weigelt, Jetz & Kreft, 2013), they were relatively over-represented. In insular studies, EH was mainly quantified through topography measures (55.8% of the insular studies), whereas mainland studies mostly involved land cover EH (50.4% of the mainland studies).

(b) Study taxa and subject areas

About one-fifth of the studies considered multiple taxonomic groups. Sixty-seven studies analysed plants and 135 analysed animals (85 vertebrates, 56 invertebrates; Fig. 2). Compared to their documented and estimated total biodiversity, invertebrates are heavily under-represented, which has also been found for macroecological studies (Beck *et al.*, 2012). This trend might partly be due to the fact that small-scale

studies were excluded from the comparison, but Tews *et al.* (2004), who considered small-scale EH, found the same bias. Most plant studies included various life forms (68.7% of the plant studies), with similar proportions analysing herbaceous (22.4%) or woody plants (23.9%) separately. Birds were by far the most frequently investigated vertebrate group (63.5% of all vertebrate studies), followed by mammals (34.1%) and reptiles (12.9%). Most invertebrate studies involved butterflies (32.1% of all invertebrate studies) or beetles (26.8%).

Plant richness was mostly studied with respect to land cover and topographic EH (52.2 and 47.8% of the plant studies, respectively). Vertebrate richness was mainly studied with regard to vegetation EH (47.1% of the vertebrate studies), closely followed by land cover and topographic EH (43.5% each), whereas invertebrate studies focused mainly on land cover (53.6% of the invertebrate studies) and vegetation EH (46.4%). Overall, studies considering land cover EH represented the largest portion of our dataset (47.9% of all studies), followed by studies considering topographic (38.5%) and vegetation EH (35.4%; 21.4% vegetation structure and 19.3% plant diversity). Vegetation EH was most frequently studied for birds and invertebrates (39.7 and 38.2%, respectively, of the studies on vegetation EH; Fig. 3), with bird richness being analysed more often in relation to vegetation structure and invertebrate richness more often in relation to plant diversity. This is not surprising as both groups depend more or less directly and strongly on vegetation, both for nesting and roosting sites and for food resources (Novotny *et al.*, 2006; Kissling, Field & Böhning-Gaese, 2008). Although climate is considered in many ecological studies (Field *et al.*, 2009), climatic EH was surprisingly scarce in our dataset. Studies with a focus on climatic or soil EH only constituted 5.7 and 8.3% of the whole dataset, respectively, and mostly analysed effects on plant richness (54.5 and 56.3% of the respective studies; Fig. 3). Again, this bias might be partly due to our selection criteria, as more soil studies may be found at smaller spatial scales, for instance.

(c) Habitat types

EH–richness studies covered all major biomes and many different habitat types from desert and tundra to tropical rainforest. Almost half of the studies covered multiple habitat types (47.4% of all studies; Fig. 2). This is not surprising because many of the studies explicitly analysed between-habitat heterogeneity or studied EH over large spatial scales. Topographic EH was the most frequently studied subject area in studies spanning multiple habitat types (54.9%). This supports the notion that topographic measures are often indirect and used as proxies for land cover, soil, or climatic EH.

Studies focusing on a single habitat type showed a large preference for forests and woodlands (29.7% of all studies). Here, EH mainly related to vegetation EH (54.4% of the studies in forests and woodlands) and was mostly analysed with regard to birds, plants, or invertebrates (35.1, 31.6, and 28.1%, respectively). These results confirm findings of Tews *et al.* (2004), who also stated a clear bias towards

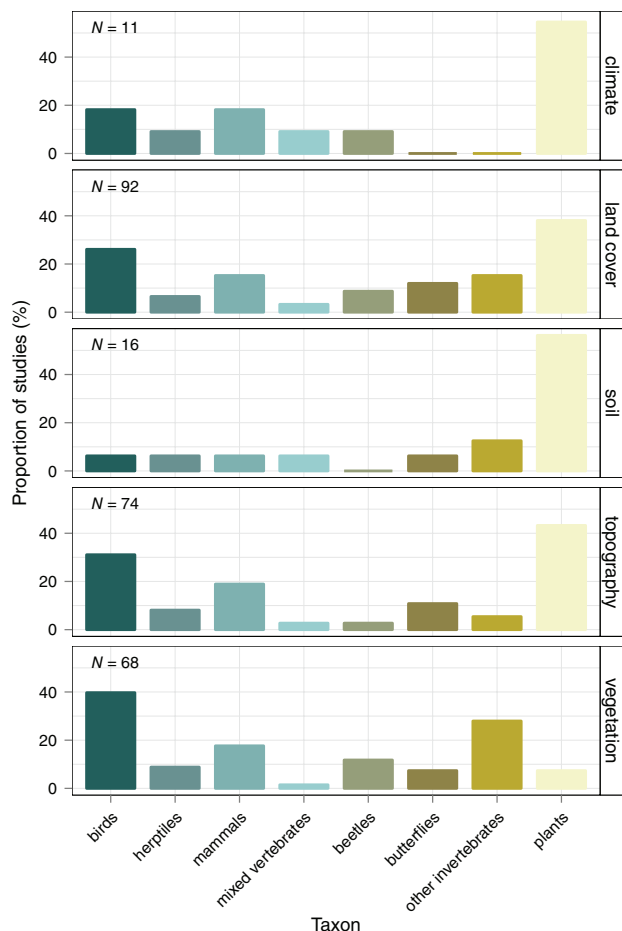


Fig. 3. Proportion of studies analysing species richness of various taxonomic groups in relation to environmental heterogeneity (EH) distinguished by subject area. The 100% reference level for each panel is N , the total number of studies considering climatic, land cover, soil, topographic, and vegetation EH, respectively.

forest systems while focusing only on vegetation EH. Martin, Blossey & Ellis (2012) similarly reported a distinct over-representation of ecological studies in temperate woodlands. The second most frequently analysed habitat type was agricultural systems (9.4% of all studies). The majority of studies in agricultural systems focused on invertebrates (44.4%) and plants (38.9%) and was situated in the Palaearctic (83.3%). By contrast, grassland studies (only 8.3% of all studies) were mostly conducted in the Afrotropic (31.3% of all grassland studies), whereas six of the nine studies involving xeric environments were located in the Nearctic. In contrast to forest systems, measures analysed in agricultural and grassland systems related to land cover EH in most studies (77.8 and 62.5% of the studies in agricultural and grassland systems, respectively).

(d) Spatial scales

EH may influence species richness over different spatial scales, which was reflected by a wide range of extent and grain

sizes in our dataset. Spatial extent varied from 10 km², i.e. the lower extent limit as defined by our inclusion criteria, to the global scale and differed among subject areas and taxonomic groups. Topographic EH was mostly quantified at regional to global extents (77.0% > 10⁴ km², 35.1% > 10⁶ km²; Fig. 2), while land cover studies focused more on a landscape extent (62.0% < 10⁴ km²). This difference is not surprising considering the large amount of large-scale topographic data available from maps, geographic information systems or the literature, whereas studies on land cover EH often rely on field data or smaller scale vegetation maps. Studies on invertebrate richness mostly focused on a landscape extent (66.1% < 10⁴ km²), whereas studies conducted at continental to global extents mainly considered vertebrate richness (71.9% of the studies conducted at > 10⁶ km²).

Our dataset also varied highly in spatial grain sizes, ranging from 1 m² plots to 5° grid cells and islands or political provinces of more than 10⁵ km² area. In small-grain studies, the most frequently analysed group were invertebrates (45.0% of all studies conducted at grains ≤ 0.01 km²), while vertebrate studies made up 55.6% of the studies conducted at grains > 100 km². Again, the differences in extent and grain sizes across taxa can partly be explained by the underlying data. The proportion of invertebrate studies using field data was distinctly higher (75.0%) than that of vertebrate studies (55.3%) which is certainly due to the greater availability of broad-scale range maps and other resources for vertebrates (e.g. Currie, 1991; Danell, Lundberg & Niemelä, 1996). Woody plants tended to be studied at larger spatial grains than herbs (largest fraction, i.e. 50.0% of woody plant studies > 100 km², 46.7% of herb studies < 1 km²). This is not surprising because, for one thing, woody plant richness, in contrast to herb richness, was partly derived from range maps that often cover relatively large areas and allow for flexible grain sizes. For another thing, field data for woody plants are often collected from larger plots than those for herbs. Fourteen studies explicitly compared multiple spatial grains or extents, mostly for measures of land cover EH. As the effects of EH are scale dependent (e.g. Böhning-Gaese, 1997; van Rensburg *et al.*, 2002; Stein *et al.*, 2014), multi-scale comparisons should offer more precise insights about EH–richness relationships than studies conducted at a single scale.

(4) Terms for EH in the literature

The afore-mentioned inconsistency in terms and concepts was confirmed by 130 different terms for EH in our dataset. Ninety-nine of these could be linked to one or more specified measures, while the others occurred only in the context of a citation or general discussion. Combining equivalent terms like ‘ecologic/ecological diversity’, ‘topographic variability/variability in topography’ or ‘vegetation/vegetational/vegetative structure’ resulted in 83 unique terms for EH that we could associate with at least one measure (see Fig. 4 and online Table S1). The most frequent term for EH was ‘habitat diversity’ (Fig. 4), which occurred (linked to a measure) in 59 studies. Forty-two studies dealt with

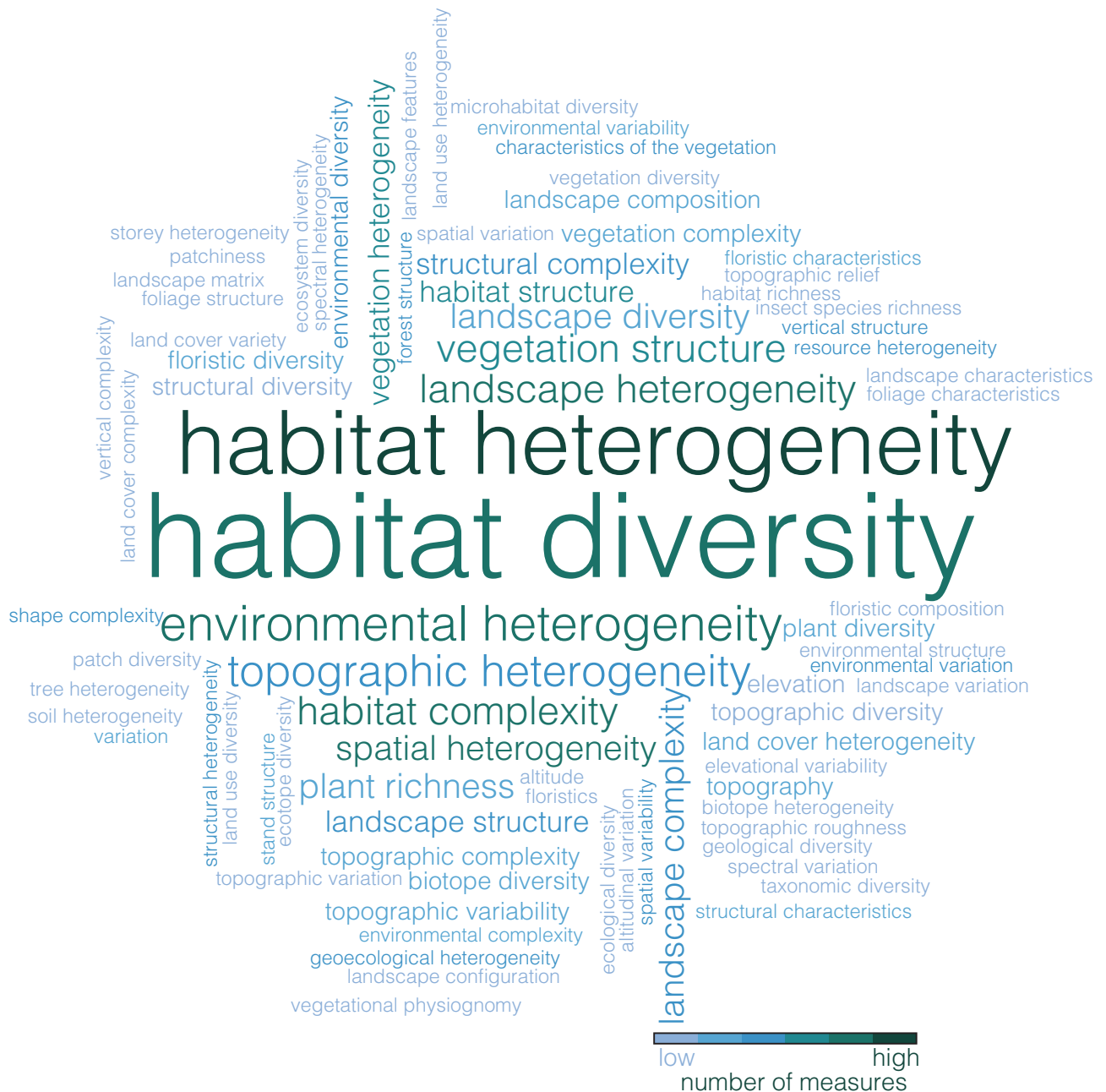


Fig. 4. Terms for EH used in our dataset that could be associated with a measure in at least one study. Font size is proportional to the number of studies using each term. Colour ramp signifies the number of measures used to quantify each term (six classes: 1–2, 3–5, 6–9, 10–19, 20–29, 42 measures).

‘habitat heterogeneity’, while ‘environmental heterogeneity’, ‘topographic heterogeneity’, and ‘landscape heterogeneity’ occurred in 19, 15, and 13 studies, respectively. Other frequently used terms were ‘habitat complexity’ and ‘vegetation structure’ (12 studies each), ‘spatial heterogeneity’ (11), and ‘landscape complexity’ (10 studies).

Terms containing ‘complexity’ or ‘structure’ mainly referred to within-habitat EH in vegetation, for instance ‘habitat complexity’ (83.3% of the respective studies), ‘habitat structure’ (75.0%), ‘structural complexity’ (87.5%),

and all occurrences of ‘environmental structure’, ‘structural diversity/heterogeneity’, and ‘vegetation/vertical structure/complexity’. In a landscape context, however, ‘landscape complexity’ and ‘landscape structure’ described between-habitat variability in all cases, mostly referring to land cover composition. The literature is thus only partly in accordance with August (1983) in his definition of ‘complexity’ as vertical stratification within a habitat and ‘heterogeneity’ as horizontal variation. This is not surprising because landscape structure and vegetation structure inevitably relate

to different features (compare McGarigal & Marks, 1995; Turner *et al.*, 2001). However, the reported trends show that the use of terms is always closely linked to the study system at hand, which can lead to confusion when comparing across different systems.

Concerning the EH subject areas, ‘habitat diversity’ was most often used to refer to land cover EH (66.1% of the studies using ‘habitat diversity’), followed by topographic EH (30.5%). ‘Habitat heterogeneity’ showed a similar trend without such a pronounced distinction (land cover EH: 47.6%; topographic EH: 42.9% of the respective studies). Climatic EH was mostly referred to as ‘habitat heterogeneity’ (45.5% of the studies about climatic EH), whereas the largest fraction of studies quantifying soil EH used the term ‘environmental heterogeneity’ (25.0%). The frequent use of the same terms implies an assumption of similar processes underlying the influence of EH across subject areas.

The majority of studies included more than one term; some contained even nine or ten. In studies where terms do not explicitly refer to specific measures (e.g. Poggio, Chaneton & Ghersa, 2010), it is difficult to determine whether numerous terms are interchangeable or what the exact differences are. Beside the terms used by the authors themselves (as, in the given example, ‘environmental heterogeneity’, ‘farmland complexity’, ‘habitat complexity’, ‘habitat heterogeneity’, ‘land-cover heterogeneity’, ‘landscape complexity’, ‘landscape composition’, ‘landscape heterogeneity’, ‘structural complexity’), additional terms often occurred only in the context of a citation (e.g. ‘landscape structure’), resulting in even more terms.

The variety, poor definition, and inconsistent use of terms impede understanding and cross-study comparisons on the topic. Ambiguous terminology is likely to hinder scientific progress by preventing relevant data from being discovered or by causing redundant research efforts to occur (Madin *et al.*, 2008). Even a term as frequent in the ecological literature as ‘habitat’ has varying and sometimes only vague definitions (Triantis *et al.*, 2003). Terminology can be further complicated through translations between different languages (McVicar & Körner, 2013). We thus encourage authors to provide clear definitions of terms and to avoid the unnecessary use of synonyms. In a scientific context, linguistic precision is more important than style and should not suffer because authors wish to avoid word repetition for the sake of variety.

(5) Quantification of EH

(a) Measures

EH has been quantified by a wide array of measures. Overall, we compiled 357 different measure names from our dataset, although many were synonyms. For instance, the measure ‘elevation range’ was also called ‘altitude’, ‘altitude/altitudinal range’, ‘elevation’, ‘elevation variability’, ‘range of variation of elevation’, ‘relief’, ‘topography’, ‘topographic range/relief’, ‘greatest/maximum elevation’ or ‘insular/island height’, when relating to islands. Instead of

‘number of habitat types’, studies also contained the names ‘habitat diversity’, ‘habitat number’, ‘habitat richness’, ‘heterogeneity of the habitat’, ‘index of number of habitat types’, or ‘number of habitats’. We combined synonyms and variants of measures, such as the number of habitat/land cover/land use/plant community types or the number of tree/tree and shrub/shrub/coniferous tree/paperbark tree species to a single measure each (in this case, number of land cover types and number of woody plant species). This resulted in 165 unique measures with varying numbers of variants per measure (see online Table S1). We could have combined measures slightly differently, which would have led to other figures than those presented here. The overall trends, however, should remain similar. We tried to achieve a reasonable overview taking the variable ecological settings of studies into account; for instance, the number of bird-dispersed plant species and the number of caterpillar food plant species both refer to species of food plants.

Overall, the most common measure was elevation range (56 studies), followed by the number of land cover types (31 studies), measures relating to the number of plant species (31 studies, compare online Table S1), and the Shannon index of land cover types (29 studies). Twenty-six measures were used in only two studies, and 109 measures in one study each. Approximately half of the studies compared multiple measures or measure variants. Deriving multiple measures from a single dataset is often easy to achieve and should offer more detailed insights into the processes underlying EH–richness relationships than studying a single measure only.

With regard to EH subject areas, we detected clear differences in the variety of measures in use, reflecting the varying number of studies in our dataset. At the spatial scales considered here, we only compiled 11 measures of climatic EH and 12 measures of soil EH. The most frequent measure of climatic EH was precipitation range (45.5% of the studies on climatic EH), followed by temperature range (36.4%). The largest portion of studies on soil EH analysed the number of soil types (37.5% of the respective studies). The aforementioned prominence of elevation range in the dataset is reflected by its use in three-quarters of the topography studies, which is not surprising because it is relatively simple to derive from maps and digital elevation models. The second most frequent measure of topographic EH, standard deviation of elevation, only occurred in 8.1% of the respective studies. We recorded 18 further measures of topographic EH, but most were only used in a single study each. Land cover EH, on the other hand, was quantified by a larger variety of measures. Here, we detected 54 different measures with a strong tendency towards diversity indices of land cover types (41.3% of land cover studies; mostly Shannon index: 31.5%) and the number of land cover types (33.7%). Percentage cover of a particular land cover type was used in 18.5% of the land cover studies. Measures of vegetation EH were even more diverse: We recorded 65 measures in total. Fifty-two measures referred to vegetation structure, the most frequently used measure being foliage height diversity (14.6% of the studies on vegetation

structure). Thirteen measures related to plant diversity, with most studies counting species of different plant groups, e.g. number of vascular plant species or number of tree species (83.8% of the studies on plant diversity).

The most frequent data sources for EH measures were field data (mainly for vegetation EH), database and literature data, maps (mainly land cover and topographic EH), digital elevation models (topographic EH), and remote sensing data (mainly land cover EH). The provenance of data partly explains the varying number of measures across subject areas: fieldwork allows for more flexibility in deriving measures than extracting data from maps, which only offer some types of information.

Terms were not matched consistently with particular measures, but each term was used in combination with many different measures and *vice versa*. This also shows that the concepts of how terms should be differentiated with respect to their meaning vary among researchers. The term ‘habitat diversity’ was most often used in combination with the number of land cover types or elevation range (22 and 15 studies, respectively). Elevation range was furthermore used frequently as a measure of ‘habitat heterogeneity’, ‘topographic(al) heterogeneity’, and ‘environmental heterogeneity’ (14, 10, and 9 studies, respectively). Of the most frequently used terms for EH, ‘habitat heterogeneity’ was quantified by 42 different measures, ‘habitat diversity’ by 27, and ‘landscape/environmental/spatial heterogeneity’ or ‘habitat complexity’ by 23–24 measures each (Fig. 4).

To make matters more complicated, what is used as a term for EH in some studies is used as a measure name in others. For instance, ‘habitat diversity’ is one of the most frequent terms for EH, which has been quantified by various measures. Steffan-Dewenter (2002) and Poggio *et al.* (2010), however, used ‘habitat diversity’ ‘as a measure of landscape complexity’. The variability in names used for equivalent measures and terms makes it difficult to find, compare, and generalize studies. Moreover, plant diversity measures, such as the number of vascular plant species, are used as EH measures in some studies, but as response variables in others. Some of the measure names are furthermore imprecise or unspecific. For instance, in other contexts, ‘elevation’ or ‘altitude’ are generally used for absolute elevation or altitude values instead of elevation range, as was the case in our dataset. Besides, it is important to distinguish between the two terms, and studies referring to mountain ranges should correctly use ‘elevation’ and not ‘altitude’ (McVicar & Körner, 2013). ‘Topography’, on the other hand, is usually more comprehensive than the mere range in elevation and can relate to other surface characteristics, such as aspect or slope, as well. Certainly, a standardized terminology is difficult to achieve for highly variable and complex measures used in different environmental settings. Still, wherever possible we would like to encourage the use of a clear terminology that makes the underlying methods transparent, replicable and comparable. For instance, we would prefer the use of ‘elevation range’ over imprecise terms like ‘topography’ or ‘elevation’, or the use of ‘number of habitat types’ over ‘habitat diversity’ (which could also signify a

diversity index of habitat types or a term for EH quantified by other measures) or ‘number of habitats’ (which is ambiguous as it might also refer to the number of habitat patches).

(b) Calculation methods

The variety of measures is reflected not only in their varying data sources, but also in their calculation methods. We found 18 different calculation methods (see Fig. 5 and online Fig. S1), with more than half of all measures being either count (13.3% of all measures), percentage (11.5%), or index measures (29.1%). The latter include diversity indices (e.g. Simpson or Shannon index) and various other complex formulae (e.g. index of precipitable water variation: Brunet & Medellín, 2001) and therefore represent the most variable calculation method. By contrast, only 4.8% of all measures

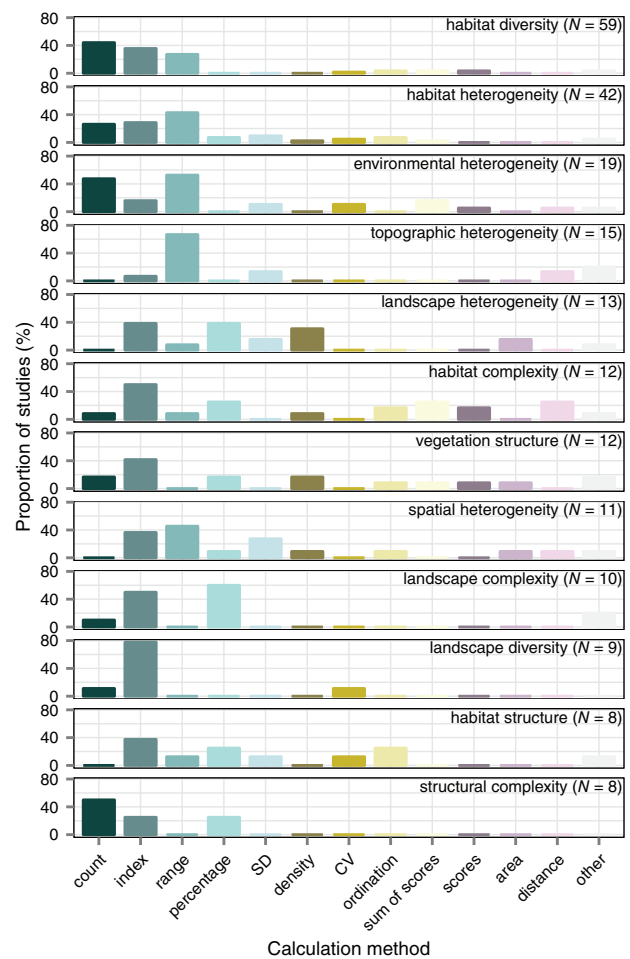


Fig. 5. Proportion of studies using different calculation methods for the quantification of environmental heterogeneity (EH) in combination with a given term for EH. Only the most common terms are displayed in the order of their frequency. The term ‘plant richness’ ($N = 9$) only occurred in combination with count measures and was omitted for clarity. The 100% reference level for each panel is N , the total number of studies using each term. Calculation methods: SD, standard deviation; CV, coefficient of variation; ‘other’ combines various rare calculation methods.

were quantified as ranges. Still, range measures were among the most frequently used, only third to count and index measures (32.3, 35.9, and 33.3% of all studies, respectively; see online Fig. S1). This is consistent with the finding that elevation range was the most frequently used EH measure, while only few other range measures have been used. Ten calculation methods were each applied in less than 4% of all measures, nine in less than 4% of all studies.

Different calculation methods contain varying information content and are likely to capture different mechanisms of EH. For instance, counts or percentages of land cover types represent the mere composition of an area, whereas indices can provide more insight into the evenness or configuration of land cover types, including potential effects of patch dynamics and fragmentation (compare McGarigal & Marks, 1995; Fahrig, 2003). Range measures in turn refer to the length of gradients but do not represent spatial variability inside study units. For instance, elevation range contains information on the strength of climatic gradients (Ruggiero & Hawkins, 2008) but does not indicate changes in slopes and aspects or the potential number of isolated valleys. As each calculation method has its own merits, comparison or combination of measures using various calculation methods should again be the most useful approach for understanding the effects of EH on species richness and other ecological target variables.

Similarly to the measures, terms for EH were not matched consistently with particular calculation methods, although some trends emerged. Terms containing 'diversity' referred to count or index measures in 39.0% and 32.0% of studies, respectively (see online Fig. S2). While count measures made up the largest portion of studies quantifying 'habitat diversity' (44.1%), index measures were by far the most frequent measures of 'landscape diversity' (77.8%, Fig. 5). Terms comprising 'heterogeneity', e.g. 'habitat heterogeneity', 'environmental heterogeneity', 'topographic heterogeneity', or 'spatial heterogeneity', were mostly used to discuss range measures (42.9, 52.6, 66.7, and 45.5% of the studies using each term, respectively), except for 'landscape heterogeneity', which was mostly quantified by index and percentage measures (38.5% each) (Fig. 5). A further deviation of terminology in the landscape context becomes apparent in the quantification of complexity and structure. While 'habitat complexity' was quantified by indices in the largest portion of the respective studies (50.0%, Fig. 5) and measures (23.1%), the main calculation method for 'landscape complexity' were percentages (60 and 50% of the respective studies and measures). A similar difference existed between the quantification of 'habitat structure' (44.4% index measures) and 'landscape structure' (50% percentage measures). Correspondingly, studies using percentage measures were conducted at a landscape extent ($\leq 10^4 \text{ km}^2$) in 76.9% of the respective studies. By contrast, there was no particular spatial focus for index and count measures, while range measures were mainly used at regional to global extents (10^4 – 10^6 km^2 : 40.3% of the studies using range measures; $> 10^6 \text{ km}^2$: 41.9%). A similar pattern held for the spatial grain, where 84.6% of the studies using percentage measures were conducted using relatively

small grains ($\leq 1 \text{ km}^2$), whereas range measures were mostly used at larger spatial grains (71.0% $> 100 \text{ km}^2$). These trends are again in accordance with the underlying data, as it is easier to derive large-scale measures from literature data and maps and small-scale measures from high-resolution field data than *vice versa*. Percentage measures were mostly derived from field data of EH and related to field data of species richness, while range measures were calculated from literature data and maps and related to species data from literature or databases (mostly species lists or range / grid maps) in the largest portion of the respective studies.

Regarding EH subject areas, climatic and topographic EH were mostly quantified by range measures (72.7 and 75.7% of the respective studies; Fig. 6). Soil and vegetation EH were mostly quantified by count measures (43.8 and 50.0%, respectively), whereas vegetation structure, when separated from plant diversity (83.8% count measures), was mostly quantified by index measures (41.5%). The largest portion of studies on land cover EH used index measures (43.5%), followed by count measures (37.0%).

We did not find distinct patterns concerning the use of calculation methods over time. The relative proportion

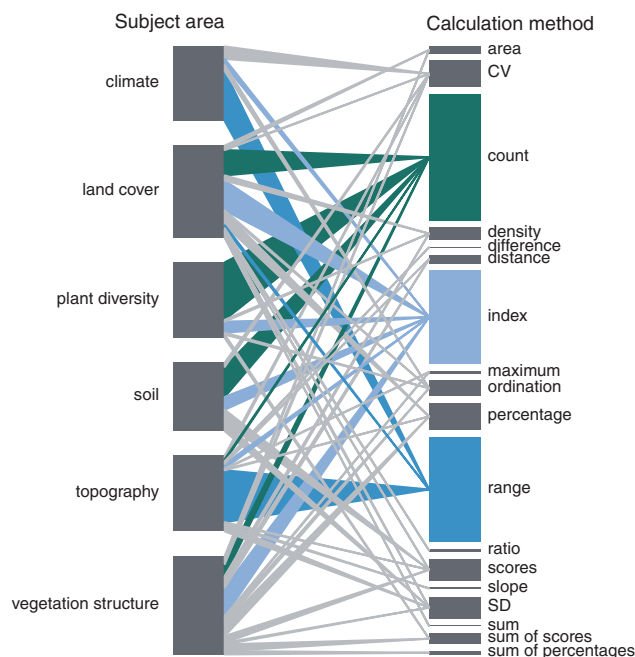


Fig. 6. Occurrence of calculation methods in environmental heterogeneity (EH) measures according to subject area. Plant diversity and vegetation structure are treated as separate subject areas to show the differences in calculation methods. Line width is proportional to the number of studies applying each particular calculation method for quantification of EH in a given subject area. For instance, plant diversity is quantified by count measures in the majority of cases, whereas topographic EH is mostly quantified by range measures. Bar height is proportional to the number of studies using each calculation method. The three most frequent calculation methods are highlighted by colour. Abbreviations: SD, standard deviation; CV, coefficient of variation.

of studies applying each method fluctuated over the past decades (see online Fig. S3). The use of standard deviations, coefficients of variation, and percentages showed a slight increasing trend, which coincided with a growing prevalence of geographic information systems and remote sensing data in the quantification of EH.

(6) Mechanisms driving EH–richness relationships

Positive relationships between EH and species richness have been attributed to various mechanisms. The most common explanation is an increase in available niche space that allows more species to coexist (e.g. Currie, 1991; Kissling *et al.*, 2008). However, the positive relationship between EH and species richness has also been suggested to result from historical factors involving species isolation or survival opportunities and thereby speciation and extinction (e.g. Durães & Loiselle, 2004; Fløjgaard *et al.*, 2011). EH may thus impact species richness through ecological as well as evolutionary processes.

Negative and unimodal EH–richness relationships have also been found in empirical studies as well as in simulation models (Tews *et al.*, 2004; Allouche *et al.*, 2012), but appear to be rare overall (Stein *et al.*, 2014). Negative relationships have frequently been attributed to fragmentation and seem to occur particularly at small spatial scales (Tews *et al.*, 2004; Tamme *et al.*, 2010; Fahrig *et al.*, 2011; Laanisto *et al.*, 2013). Another reason why EH is not necessarily positively linked with species richness is a reduction of suitable area available to each species that may be associated with increasing EH, which in turn should increase the likelihood of stochastic extinctions (Kadmon & Allouche, 2007). The debate about this issue is still ongoing (e.g. Allouche *et al.*, 2013; Hortal *et al.*, 2013), and further research is needed to substantiate the area–heterogeneity trade-off (Allouche *et al.*, 2013).

Here, we concentrate on the mechanisms behind positive EH–richness relationships. We distinguish three main aspects through which EH may positively affect species richness, namely through the promotion of (i) species coexistence, (ii) species persistence, and (iii) species diversification (Table 3). The underlying processes operate at different spatial and temporal scales. Processes involving the impact of local-scale habitat structure and interactions on coexistence within communities are likely to occur at time scales of several to a hundred years (Willis & Whittaker, 2002). At a landscape scale, land cover, soil, or topographic EH may affect species turnover at the scale of centuries to millennia (Willis & Whittaker, 2002). At larger spatial scales, topographic EH can promote allopatric speciation and ecological speciation, which may require hundreds of thousands of years (Rosenzweig, 1995).

The influence of EH is also taxon dependent. From an ecological point of view, specific habitat requirements and functional traits, such as body size or mobility, determine whether a species perceives its environment as heterogeneous and whether it benefits from EH or suffers from fragmentation, for example (Huston, 1994; Tews *et al.*, 2004). Also plant size in relation to patch size is important for




the perception of EH by individual plants (Hutchings, John & Wijesinghe, 2003; Tamme *et al.*, 2010). Furthermore, species richness of habitat specialists may be linked more closely to EH than that of habitat generalists (Ricklefs & Lovette, 1999; Menendez *et al.*, 2007). Since habitat specialists depend on the availability of a certain habitat type or element, the prevalence of multiple diverse habitat types should allow differently specialized species to coexist and might even give them a competitive advantage over generalists. However, the opposite has been argued as well because generalists should be able to gain resources from more than one habitat type and may therefore benefit more from EH (Jonsen & Fahrig, 1997; Batáry *et al.*, 2007). Oliver *et al.* (2010) reported different impacts of EH on the stability of specialist and generalist populations depending on spatial scale. Overall, areas with larger EH may be more likely to meet the habitat requirements of both generalist and specialist species (Kumar, Simonson & Stohlgren, 2009). In an evolutionary context, diversification rates in response to EH and the susceptibility to geographic barriers, resulting e.g. from topographic EH, differ among taxa as well. Moreover, the probability of encountering a barrier that might lead to allopatric speciation should be larger for species with larger range sizes, while at the same time the barrier may be less likely to cut through the range completely (Rosenzweig, 1995).

Almost half of the studies in our dataset did not refer to any theories about mechanisms behind EH–richness relationships. On one hand, this was because EH was not the main focus but rather a side aspect in many studies. On the other hand, ecological literature in general has been found bereft of theory (Scheiner, 2013), and the lack of links to ecological theory in EH–richness studies surely hampers acquisition of scientific knowledge in this field. Of the 107 studies that did include theories, the vast majority (96 studies) discussed EH–richness relationships in the light of species coexistence mechanisms. Thirty-one studies referred to mechanisms related to species persistence, while only 11 studies addressed mechanisms related to diversification.

(a) Species coexistence

The largest portion of our dataset, i.e. 86 studies, related to the theory that an increase in available niche space and more diverse resources due to increasing EH allow more species to coexist (e.g. Kissling *et al.*, 2008; Fløjgaard *et al.*, 2011). The majority of these studies analysed vertebrate richness and were conducted at relatively small spatial grains and extents (Table 3). EH–richness relationships in this context can be related to the following processes. First, an increase in plant diversity represents an increase in resource diversity for herbivores, which should usually allow more consumer species to coexist (Hutchinson, 1959). This is because the higher the number and variety of plant resources, the higher the probability that a particular resource is available to a particular consumer. Herbivore diversity should thus be directly promoted by plant diversity. This relationship has been found for insects (Chown, Gremmen & Gaston, 1998; Novotny *et al.*, 2006;

Table 3. Potential mechanisms behind positive environmental heterogeneity (EH)–richness relationships mentioned in the literature. We classified mechanisms according to the three main aspects species coexistence, persistence and diversification.

	Mechanism	EH subject area	Taxon	Habitat type	Spatial scale
Coexistence	More opportunities to coexist through more potential niches and diverse resources such as food and colonization, mating, oviposition, breeding, foraging and roosting sites	Vegetation (43), land cover (37), topography (34), soil (9), climate (6)	Vertebrates (40), plants (29), invertebrates (26)	Mixed (35), forest (30), agricultural (7), grassland (7), xeric (6), montane (1)	
	Spatial turnover of species favouring different habitat types or abiotic conditions (e.g. energy or water availability, soil pH or compaction)	Land cover (5), topography (5), soil (2), climate (1)	Plants (6), vertebrates (4), invertebrates (1)	Mixed (6), grassland (3), forest (1)	
Persistence	Reduced extinction risk through shelter from predators, parasites and harsh abiotic conditions such as cold or heat	Land cover (10), vegetation (10), soil (2), topography (1)	Invertebrates (12), vertebrates (5), plants (1)	Forest (7), agricultural (5), mixed (4), grassland (1)	
	Reduced extinction risk through reduced competitive pressure	Vegetation (3), topography (2), land cover (1)	Vertebrates (3), plants (2), invertebrates (2)	Mixed (3), forest (1), grassland (1)	
	Survival of populations through vertical range shifts and refuges in periods of adverse environmental conditions	Topography (8), land cover (3), soil (2), climate (1), vegetation (1)	Plants (4), vertebrates (4), invertebrates (2)	Mixed (7), forest (1), xeric (1)	
Diversification	Divergent natural selection, specialization and adaptive radiation through diverse environmental pressures and opportunities	Topography (5), land cover (3), soil (2), vegetation (2), climate (1)	Plants (3), vertebrates (3), invertebrates (2)	Mixed (5), forest (2)	
	Allopatric speciation through isolation of populations by physically or physiologically effective barriers	Topography (7), vegetation (3), soil (2), climate (1), land cover (1)	Plants (4), vertebrates (4), invertebrates (1)	Mixed (6), forest (2)	

The numbers in parentheses indicate the numbers of studies (in decreasing order) mentioning each mechanism and investigating a particular EH subject area, taxon and habitat type. Within each aspect, the different mechanisms are ordered according to an increasing spatial scale, i.e. grain and extent, as indicated by the triangles.

Kumar *et al.*, 2009), birds (Seto *et al.*, 2004), and vertebrates (Qjan & Kissling, 2010). In this context, not only species richness of plants is important, but also functional diversity. For instance, frugivorous birds, although rarely specialized on fruits of one particular plant species, are often adapted to particular fruit types, sizes, colours, or modes of presentation (Kissling, Rahbek & Böhning-Gaese, 2007; Kissling *et al.*, 2008). Plant diversity can also indirectly promote predator diversity through its impact on herbivorous prey and bottom-up trophic cascades (Chown *et al.*, 1998; Scherber *et al.*, 2010). Animals, fungi, or microorganisms can promote EH through trophic interactions, pollination networks, symbiosis, facilitation, parasitism, or activities such as grazing, burrowing, or trampling (Stewart, John & Hutchings, 2000). This may lead to a positive feedback between heterogeneity and species diversity (Wilson, 2000). Second, species

coexistence of plants and soil organisms should be positively associated with soil EH, for instance heterogeneity in nutrient availability, pH, soil compaction, or water content. Microtopographically complex areas are likely to provide special habitats, such as rock crevices, gypsum outcrops or salt pans, that often harbour highly adapted and narrowly endemic species (Dinerstein *et al.*, 2000). Third, diversity of microhabitats that offer protection, foraging, roosting, breeding, and oviposition sites, or variability in light and water regimes is essential for species coexistence, as it is for species persistence. More complex vegetation is also important in this context because it provides microhabitats suitable for colonization by a larger variety of species, such as insects (Gonçalves-Alvim & Fernandes, 2001). Accordingly, the largest portion of studies referring to the presented mechanisms analysed vegetation EH, followed by land cover EH (Table 3).

At broader spatial scales, EH can promote spatial turnover of species that favour different habitat types or abiotic conditions. The 10 studies from our dataset addressing this mechanism mainly analysed land cover and topographic EH and effects on plant species richness (e.g. Deshayé & Morisset, 1988; Homeier *et al.*, 2010; Table 3). With respect to land cover EH, both land cover configuration and composition can affect species coexistence. A patchy environment should offer a wider variety in abiotic conditions (e.g. insolation, moisture, or disturbance) than a non-patchy one. It may thus promote coexistence of species with different habitat requirements, e.g. species favouring closed vegetation *versus* edge habitats (Batáry *et al.*, 2007; Kumar *et al.*, 2009). In mountain systems, the impact of topographic EH has been partly attributed to high rates of change in climatic conditions and habitat types over relatively short distances (Körner, 2000; Ruggiero & Hawkins, 2008).

(b) *Species persistence*

EH may also influence species richness through a reduction of extinction risk and promotion of population stability (Marini *et al.*, 2010), which in turn promotes species persistence. Seventeen studies included the notion that EH provides shelter from predators and unfavourable conditions like cold or heat. These studies mostly analysed land cover and vegetation EH at relatively small spatial scales and focused on invertebrate richness and forest or agricultural systems (e.g. Lassau & Hochuli, 2005; Garden, McAlpine & Possingham, 2010; Table 3). Another potential mechanism mentioned in five studies was that higher EH may reduce extinction risk due to lower competitive pressure (e.g. Heatwole, 1991). MacArthur (1972) proposed that extinction rates on islands rise abruptly as soon as all habitats are occupied by corresponding species. This implies that larger EH may result in lower extinction rates because regions with more habitat types are less likely to have all habitats occupied. However, species persistence can also be impaired by the addition of habitat types, when the associated decrease in area of habitat suitable for a particular species leads to reduced population sizes and hence to a higher risk of stochastic extinctions (Kadmon & Allouche, 2007; Allouche *et al.*, 2012; but see Hortal *et al.*, 2013).

At larger spatial scales, EH has also been related to enhanced persistence of populations in refuges from larger scale adverse environmental conditions (e.g. Kohn & Walsh, 1994). Eight out of nine studies referring to this mechanism analysed topographic EH, which may permit range shifts or contractions in response to climate change and glacial events (e.g. Kallimanis *et al.*, 2010; also see Sandel *et al.*, 2011) or to avoid competition or pathogenicity introduced by new colonists (Ricklefs & Lovette, 1999).

(c) *Species diversification*

In an evolutionary context, EH has been argued to be important through its promotion of adaptation, diversification, and speciation (Simpson, 1964). As most speciation events are

thought to occur in allopatry (Barraclough & Vogler, 2000), geographic isolation limiting gene flow between populations is an important prerequisite for diversification. Eight studies in our dataset related EH to vicariance and allopatric speciation (e.g. Andrews & O'Brien, 2000; Durães & Loiselle, 2004). These studies mostly investigated topographic EH at spatial grains >100 km² (Table 3). Regions with a high level of EH are generally more likely to contain barriers that may isolate populations than homogeneous areas. Barriers can impede gene flow between populations through two mechanisms. First, they may represent physical obstacles that are insurmountable due to the restricted mobility of organisms. The effectiveness of barriers thereby depends on taxon-specific dispersal abilities. Second, organisms may be unable to cross barriers because they are adapted to different environmental conditions (Janzen, 1967). For instance, even if an organism is physically able to cross a mountain range, it may be physiologically unable to bear the unfamiliar climatic conditions this crossing would involve. Mountainous areas are usually rich in range-restricted species that occur only on single ranges, isolated peaks or valleys. A well-known example of the effect of EH on speciation is the Andes, where recent uplift has led to a high level of topographic EH, providing many opportunities for isolation and species diversification (Antonelli & Sanmartín, 2011). The Andean uplift has been considered essential to some of the fastest and most prominent diversifications in plants (Kay *et al.*, 2005; Hughes & Eastwood, 2006), and the region is paramount in the number of native and endemic species of plants and vertebrates (Hughes & Eastwood, 2006).

Another important role of EH lies in the promotion of ecological speciation (Givnish, 2010). In this case, barriers to gene flow result from ecologically driven divergent selection (Nosil, 2012). Seven studies in our dataset related to the notion that larger EH promotes specialization and adaptive radiation through a wider variety of environmental pressures and opportunities (e.g. Kallimanis *et al.*, 2010; Table 3). In particular, the probability and extent of adaptive radiation should increase when a larger variety of resources is available for partitioning (Givnish, 2010). An iconic example of radiation driven by EH in birds is the divergent bill and tongue morphology and varying plumage colour related to diverse food resources and foraging behaviour in Hawaiian honeycreepers (Freed, Conant & Fleischer, 1987). Similarly, variety in elevation, climate, substrate, and microtopography has been deemed responsible for radiation in *Aeonium* on the Canary Islands (Lems, 1960; Givnish, 2010). Here, a plethora of species has evolved with growth forms and root morphologies adapted to different temperature and moisture regimes, soil types, and rock formations. EH, particularly in mountain systems, may therefore affect species richness through various synergistic processes, involving geographic isolation, steep climatic gradients, and the availability of diverse resources and habitat types over relatively small areas.

(7) **Confounding factors**

The mechanisms responsible for positive EH–species richness relationships are often difficult to disentangle, not

least because EH can be confounded with other variables and processes. For example, a central hypothesis for explaining species diversity patterns relates to productivity (Currie, 1991; Hawkins *et al.*, 2003). Complex vegetation structure, though a measure of EH, may also reflect increased productivity. A relationship between vegetation structure and consumer species richness may thus indicate the effect of available energy rather than EH (Nilsson, 1979). Another confounding factor is that structurally more complex plants should also be easier to find by herbivores or pollinators, so that vegetation EH might be confounded with a higher ‘apparency’ of the vegetation (Feeny, 1976; Lawton, 1983). More complex vegetation usually also entails a larger plant area, which can support more herbivores and thereby reduces extinction probabilities (Araújo *et al.*, 2006). Understanding the importance of vegetation EH is further hampered by the fact that cross-taxon relationships, e.g. correlations between plant and consumer diversity, do not necessarily result from a causal link. Instead, the taxa may depend on the same environmental factors or respond to different environmental variables that covary in space (Wolters *et al.*, 2006; Jetz *et al.*, 2009). Another instance in which our understanding of the impact of EH can be impeded is when EH is confounded with changes in mean environmental conditions. For instance, acidic patches of conifer litter can be interpreted as EH but at the same time lower the mean soil pH at a larger spatial scale (Tamme *et al.*, 2010). Higher species richness measured in more heterogeneous environments may also result from enhanced mass effects, when more individuals can immigrate from adjacent, dissimilar habitats, even though they do not form viable populations (Shmida & Wilson, 1985; Palmer *et al.*, 2002).

As EH and area are closely related, their relative contributions to species diversity patterns have received particular attention (Kohn & Walsh, 1994; Ricklefs & Lovette, 1999; Triantis *et al.*, 2003, 2005; Hannus & von Numers, 2008). Area is expected to influence species diversity through effects on immigration, extinction, and speciation rates (MacArthur & Wilson, 1963, 1967; Kisel *et al.*, 2011) or *via* an increase of EH (Williams, 1964; Johnson & Simberloff, 1974). In general, larger areas are more likely to hold a larger number of habitat types or broader gradients in environmental conditions. Certainly, the influences of area and EH complement each other (Triantis *et al.*, 2005; Hannus & von Numers, 2008). One way to account for additive effects of area and EH is to extend the power model of the species–area relationship by supplementing area with a multiplicative term of area and the number of habitat types (Triantis *et al.*, 2003). The individual effects of area and EH are often hard to distinguish, particularly as many EH measures are highly correlated with area (Ricklefs & Lovette, 1999). Also topography correlates not only with heterogeneity in environmental conditions but also with surface area (Ferrer-Castán & Vetaas, 2005). Triantis *et al.* (2008aa), however, found that the inclusion of an EH measure led to a significantly higher improvement of species richness models than substituting planar area by actual surface area of topographically diverse islands. By contrast,

Beck & Kitching (2009) reported that while surface area of elevational bands was a better predictor of species richness than planar area, they did not find any evidence for an effect of habitat heterogeneity on species–area relationships.

To minimize confounding of EH and area, it is desirable to control for direct area effects by analysing EH across units of equal or similar sizes (Stein *et al.*, 2014). The study units in our dataset included plots, grid cells, and irregular shapes, such as forest fragments, islands, nature reserves, and countries. Less than half of the studies in our review contained units of uniform area. While plots or grid cells can easily be defined as equal area units (assuming a flat plane; also see Nogués-Bravo & Araújo, 2006), varying plot sizes and grid cells delimited by degrees instead of area have also been widely used. A way to cope with differences in area of shapes such as islands has been the analysis of subsets of similar-sized units (e.g. Davidar, Yoganand & Ganesh, 2001). Controlling for area through statistical methods, by contrast, in cases seems problematic because of the above-mentioned collinearity between EH and area (compare Whittaker, Willis & Field, 2001).

III. CONCLUSIONS

(1) Environmental heterogeneity–richness relationships are a central topic in ecology and biogeography. At the same time, EH is a highly diverse topic that has motivated many different quantification methods and concepts. Despite the high variability in study settings and methodology, some clear trends emerged from our systematic literature review. (i) There is a significant bias towards studies on land cover EH in the Palaearctic and an under-representation of studies on invertebrates, climatic EH, and soil EH, at least at the scales considered here. Patterns in spatial scales, habitat types, and study taxa differ among subject areas. The fact that topographic EH is the predominant subject area in studies across multiple habitat types suggests that topographic measures are often used as proxies, e.g. for climatic or land cover EH, because direct measures of the latter are not as easily available. (ii) Considerably more measures have been used for land cover and vegetation EH than for topographic EH. Overall, the most frequently used measure was elevation range, followed by the number and diversity indices of land cover types and plant species. Despite the high variability in measures, similar calculation methods reoccur across studies. (iii) The investigated subject areas and study systems were partly associated with the assumed mechanisms behind EH–richness relationships. Most studies related to increased niche space and diverse resources provided by higher EH, which mostly involved vegetation EH in these studies. (iv) To understand better the effects of EH on species richness, future studies should include comparisons across spatial scales and across measures, involving both different subject areas and calculation methods. Besides these recommendations for future study designs, a comparative re-analysis of existing datasets evaluating multiple standardized measures has great potential for fostering synthesis.

(2) The terminology used in the context of EH is ambiguous and lacks a clear consensus about concepts and meanings of terms. There is a tendency towards the use of ‘diversity’, ‘structure’, and ‘complexity’ in relation to EH quantified by count or index measures, whereas ‘heterogeneity’ relates more often to environmental gradients quantified by range measures. By contrast, in the landscape context, percentage measures are most frequently used to quantify ‘landscape complexity/heterogeneity/structure’. These trends are impaired by the common use of synonyms without clear delimitations in many studies. We therefore encourage authors to be precise in their terminology and definitions and to avoid using multiple synonymous terms and measure names unless necessary. A consistent terminology promotes understanding, is essential for synthesis, and should foster advancement of the whole field.

(3) It was not our aim to choose or propose one single, optimal EH measure. This would in fact be highly difficult to generalize, as the most appropriate measure always depends on the study system of interest. We hope that our review will guide researchers in choosing relevant, taxon- and ecosystem-specific measures as potential proxies of the processes of interest. Distinguishing between effects of EH on species coexistence, persistence, and diversification should help to link measures with underlying mechanisms.

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V. REFERENCES

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VI. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Fig. S1. Frequency of calculation methods in studies and measures.

Fig. S2. Proportion of studies using each calculation method in combination with a particular noun for terms for EH.

Fig. S3. Proportion of calculation methods per decade.

Table S1. Measures and measure variants of environmental heterogeneity.

Appendix S1. Literature search in *Web of Science*.

Appendix S2. References.

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