Environmental heterogeneity–species richness relationships from a global perspective

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It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living.

David Attenborough

Abstract

Spatial environmental heterogeneity (EH) is regarded as one of the most important drivers of species richness gradients worldwide. Its association with increased available niche space, provision of refuges, and opportunities for diversification through isolation and divergent adaptation are thought to promote species coexistence, persistence, and diversification. The exploration of potential positive effects of EH on species richness has intrigued ecologists and evolutionary biologists for decades. Consequently, a large body of literature exists on the relationship between EH and species richness of various taxa and in diverse ecological settings. EH can involve heterogeneity in biotic and abiotic conditions and has been quantified with many different measures across a variety of spatial scales, ranging from the structural complexity of single plants to landscape structure and topographic relief. This diverse measurement and an often indistinct and inconsistent terminology used in EH–species richness research hamper the understanding, comparison and synthesis of studies. Moreover, the reported relationships between EH measures and species richness vary widely, including positive, but also non-significant, hump-shaped, and negative results. Therefore, no general consent about the overall EH–species richness relationship exists so far.

In this thesis, I conduct a systematic literature review, providing an overview of the EH measures and terms that have been used in EH–species richness research. Based on 192 studies, I identify 165 different EH measures, which I classify according to their subject area and calculation method. Five subject areas can be distinguished, i.e. land cover and vegetation as biotic components of EH, and climate, soil, and topography as abiotic components. I detect eighteen different calculation methods, such as count, standard deviation, and coefficient of variation. Elevation range emerges as the most frequently used EH measure in the literature, whereas measures of climatic and soil EH are underrepresented. Furthermore, I reveal clear spatial and taxonomic bias in research, with most studies investigating effects of EH in the Palaearctic realm and focusing on vertebrate or plant species richness. I compile more than 100 different terms for EH, such as habitat diversity and habitat heterogeneity, and reveal that they are insufficiently or even contradictorily defined in the literature. As such ambiguity hampers understanding, I call for clearer terminology and avoidance of unnecessary synonyms. I also review potential mechanisms behind positive EH–richness relationships that have been discussed in the literature. Overall, seven main mechanisms associated with a promotion of species coexistence, persistence and diversification can be distinguished, which I link to the studied EH subject areas and other study characteristics like taxon and spatial scale.

Based on the same dataset of 192 studies and 1148 data points, I then conduct a meta-analysis to explore the overall direction and strength of the relationship between EH and species richness of terrestrial plants and animals. I provide substantial, quantitative support that the relationship is generally positive across taxa, habitat types, and spatial scales from landscape to global extents. There is no significant difference in effect sizes between biotic and abiotic EH, however, vegetation and topographic EH show particularly strong associations with species richness compared with climatic EH. In a mixed-effects meta-regression approach, I identify study characteristics that affect the strength of EH–richness relationships. Spatial scale, in particular the use of equal-area study units, spatial grain, and spatial extent, emerge as key factors influencing the analysed relationship between species richness and EH measures associated with land cover and elevation.

Building on the findings from the literature review, I finally conduct a case study investigating the similarity among a range of EH measures and their effects on species richness of terrestrial mammals worldwide. I systematically calculate 51 different EH measures at global extent, covering all five EH subject areas and nine different calculation methods. I demonstrate that some of these measures are clearly distinct, whereas others are highly collinear and partly redundant. I identify similarities and differences among regions worldwide with regard to the spatial pattern of particular EH measures and multidimensional EH space based on principal component analysis. Moreover, I explore the association of each EH measure with mammal species richness in single- and multi-predictor regression models, which additionally account for the influence of current climate, biogeographic region, and human influence. Using conditional inference trees, I investigate the impact of the different subject areas and calculation methods of EH measures on model support across three spatial grains. The choice of subject area turns out to be most influential, with measures of climatic and topographic EH gaining comparatively high model support. Moreover, EH measures calculated as counts and ranges are also associated with high model support across all spatial grains, whereas coefficient of variation and terrain ruggedness index gain relatively low model support. Overall, my results highlight the high impact of methodological decisions on the outcome of EH–species richness studies. This confirms the importance of choosing meaningful, taxon- and scale-dependent EH measures for the study system and mechanism of interest.

This thesis represents the most comprehensive assessment of the measurement and terminology of EH across subject areas and taxonomic groups so far. It also provides the first quantitative support for the generality of positive relationships between biotic and abiotic EH and species richness of terrestrial taxa at relatively broad spatial scales. My research clearly demonstrates the immense complexity of EH as a topic and research field. Despite the considerable advancements in EH–species richness research made by this work, many open questions remain to be addressed. The present thesis intends to provide a solid foundation for meeting this challenge in the future.

Zusammenfassung

Heterogenität von Umweltbedingungen gilt als einer der wichtigsten Faktoren für die Verteilung von Artenreichtum weltweit. Laut der Habitatheterogenität-Hypothese bieten räumlich heterogenere Gebiete eine höhere Vielfalt an Umweltparametern und weisen mehr Refugien und Möglichkeiten zur Isolation und Radiation auf. Dadurch begünstigen sie Koexistenz, Persistenz und Diversifikation von Arten. Die Erforschung potentieller positiver Effekte von Heterogenität auf Artenreichtum fasziniert Ökologen und Evolutionsbiologen seit Jahrzehnten. Dementsprechend existieren zahlreiche Studien über die Beziehung zwischen Heterogenität und dem Artenreichum verschiedener Taxa unter unterschiedlichsten ökologischen Gegebenheiten. Heterogenität kann sich auf biotische und abiotische Bedingungen beziehen und wurde daher mittels vieler verschiedener Maße quantifiziert. Diese finden zudem auf sehr unterschiedlichen Skalen Anwendung, die von der Architektur einer einzelnen Pflanze über Landschaftsstruktur bis hin zu topographischem Relief reichen. Die Vielfalt der Maße sowie eine oft unbestimmte und inkonsistente Terminologie, die in der Forschung zu Heterogenität-Artenreichtums-Beziehungen verwendet wird, erschweren das Verständnis, den Vergleich und die Synthese der entsprechenden Studien. Desweiteren gibt es große Unterschiede in der Form und Stärke der Beziehungen: während viele Studien einen positiven Zusammenhang zwischen Heterogenität und Artenreichtum nachwiesen, sind auch negative, unimodale und nicht signifikante Zusammenhänge bekannt. Deshalb existiert bisher kein eindeutiger Konsens bezüglich der generellen Heterogenität-Artenreichtums-Beziehung.

Im Rahmen der vorliegenden Dissertation fertige ich ein systematisches Literaturreview an, mit dem ich einen Überblick über die verwendeten Maße und Begriffe gebe, die bisher in der Forschung zu Heterogenität-Artenreichtums-Beziehungen Anwendung fanden. Basierend auf 192 Studien identifiziere ich 165 verschiedene Heterogenitätsmaße, die ich bezüglich ihrer Themenfelder und Berechnungsmethoden klassifiziere. Es werden fünf Themenfelder unterschieden, nämlich Landbedeckung und Vegetation als biotische Komponenten, und Klima, Boden und Topographie als abiotische Komponenten von Heterogenität. Desweiteren identifiziere ich achtzehn verschiedene Berechnungsmethoden, wie z.B. Anzahl, Standardabweichung und Variationskoeffizient. Die Höhenspannweite in einem Gebiet erweist sich als das häufigste Heterogenitätsmaß in der Literatur, wohingegen Maße von klimatischer Heterogenität und Bodenheterogenität unterrepräsentiert sind. Weiterhin stelle ich ein deutliches räumliches und taxonomisches Ungleichgewicht in der Forschung fest, wobei ein Großteil der Studien den Einfluss von Heterogenität in der Paläarktis untersucht und sich auf den Artenreichtum von Vertebraten oder Pflanzen konzentriert. Ich kompiliere über 100 verschiedene Begriffe für Heterogenität, wie z.B. *Habitatdiversität* oder *Habitatheterogenität*, und weise auf mangelhafte und teilweise sogar widersprüchliche Definitionen hin. Solche Unklarheiten erschweren das Verständnis der Begriffe und Studien, weshalb ich für eindeutige Terminologie plädiere und mich gegen die Verwendung von Synonymen ausspreche. Desweiteren gebe ich einen Überblick über mögliche Mechanismen, die als Grundlage von positiven Zusammenhängen zwischen Heterogenität und Artenreichtum in der Literatur diskutiert werden. Insgesamt identifiziere ich sieben Hauptmechanismen, die mit der Förderung von Koexistenz, Persistenz und Diversifikation von Arten zusammenhängen. Diese Mechanismen stelle ich in Beziehung zu den Themenfeldern der Heterogenitätsmaße, den Taxa und den räumlichen Skalen, die in den jeweiligen Studien behandelt werden.

Basierend auf dem gleichen Datensatz von 192 Studien und 1148 Datenpunkten führe ich anschließend eine Meta-Analyse durch, um die generelle Richtung und Stärke des Zusammenhangs zwischen Heterogenität und dem Artenreichtum terrestrischer Pflanzen und Tiere zu untersuchen. Hierbei weise ich quantitativ nach, dass der Zusammenhang von der Landschaftsebene bis zur globalen Skala über Taxa, Habitattypen und räumliche Skalen hinweg generell positiv ist. Während kein signifikanter Unterschied in der Effektgröße zwischen biotischer und abiotischer Heterogenität besteht, weisen Vegetations- und topographische Heterogenität signifikant stärkere Assoziationen mit Artenreichtum auf als klimatische Heterogenität. Durch gemischte Meta-Regressionen identifiziere ich weiterhin Studieneigenschaften, die die Stärke des Zusammenhangs zwischen Heterogenität und Artenreichtum beeinflussen. Räumliche Skalen, insbesondere Flächenkonstanz, räumliche Auflösung und Ausdehnung, stellen sich als besonders wichtige Einflussgrößen für die untersuchte Beziehung zwischen Artenreichtum und auf Landbedeckung und Höhe basierenden Heterogenitätsmaßen heraus.

Ausgehend von den Ergebnissen des Literaturreviews untersuche ich schließlich die Ähnlichkeit zwischen einer Reihe von Heterogenitätsmaßen sowie deren differentiellen Einfluss auf den globalen Artenreichtum terrestrischer Säugetiere. Ich berechne systematisch 51 verschiedene Heterogenitätsmaße auf globaler Ebene, die alle fünf Themenfelder von Heterogenität abdecken und neun verschiedene Berechnungsmethoden beinhalten. Ich zeige, dass manche dieser Maße sich deutlich voneinander abheben, während andere stärker kollinear und zum Teil redundant sind. Ich stelle Ähnlichkeiten und Unterschiede zwischen verschiedenen Regionen in Bezug auf räumliche Muster einzelner Heterogenitätsmaße sowie einen multidimensionalen Heterogenitätsraum heraus, der auf einer Hauptkomponentenanalyse beruht. Außerdem untersuche ich den Zusammenhang zwischen jedem einzelnen Heterogenitätsmaß und dem Säugetierreichtum in einfachen und multiplen Regressionsmodellen, welche zusätzlich den Einfluss von Klima, biogeographischer Region und menschlichem Einfluss berücksichtigen. Mit Hilfe von bedingten Inferenzbäumen analysiere ich den Einfluss der verschiedenen Themenfelder und Berechnungsmethoden der Heterogenitätsmaße auf die Modellgüte über drei räumliche Auflösungen hinweg. Die Wahl der Themenfelder stellt sich dabei als wichtigster Einflussfaktor heraus, wobei sich Maße klimatischer und topographischer Heterogenität besonders positiv auf die Modellgüte auswirken. Desweiteren zeichnen sich Modelle mit Anzahl- oder Spannweitemaßen ebenfalls durch hohe Modellgüte aus, wohingegen der Variationskoeffizient und ein Geländeschroffheitsindex mit relativ geringer Modellgüte zusammenhängen. Insgesamt betonen meine Ergebnisse die hohe Bedeutung methodischer Entscheidungen auf die Ergebnisse von Heterogenität-Artenreichtums-Studien. Dies wiederum dokumentiert wie wichtig es ist, sinnvolle, taxon- und skalenabhängige Heterogenitätsmaße zu verwenden, die dem jeweiligen Untersuchungssystem und dem zu untersuchenden Mechanismus entsprechen.

Diese Dissertation stellt die bisher umfangreichste Untersuchung der Quantifizierung und Terminologie von Heterogenität über Themenfelder und verschiedene taxonomische Gruppen hinweg dar. Sie belegt erstmals einen generell positiven Zusammenhang zwischen biotischer und abiotischer Heterogenität und dem Artenreichtum terrestrischer Pflanzen und Tiere auf

relativ großen räumlichen Skalen. Meine Forschung demonstriert deutlich die enorme Komplexität von Heterogenität als Thema und Forschungsgebiet. Trotz der beachtlichen Fortschritte, die durch diese Arbeit in der Erforschung von Heterogenität-Artenreichtums-Beziehungen gemacht wurden, gilt es noch zahlreiche offene Fragen zu beantworten. Die vorliegende Dissertation soll eine solide Basis schaffen, um diese Herausforderung in Zukunft anzugehen.

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Author contributions

Chapter 2: Terminology and quantification of environmental heterogeneity in species-richness research

The following authors contributed to this chapter: Anke Stein[1] and Holger Kreft[1]. AS and HK designed the study; AS compiled and reviewed the literature; AS collected and analysed the data and wrote the manuscript with substantial contributions from HK.

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Chapter 3: Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales

The following authors contributed to this chapter: Anke Stein[1], Katharina Gerstner[2] and Holger Kreft[1]. HK conceived the idea; AS and HK designed the study; AS compiled and reviewed the literature; AS collected the data and performed the analysis with substantial contributions from KG; AS wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Chapter 4: Differential effects of environmental heterogeneity on global mammal species richness

The following authors contributed to this chapter: Anke Stein[1], Jan Beck[3], Carsten Meyer[1], Elisabeth Waldmann[4], Patrick Weigelt[1,5] and Holger Kreft[1]. AS, JB, CM, PW and HK designed the study; AS compiled the data with substantial contributions from CM, PW and HK; AS and EW analysed the data with major assistance from CM, PW and HK; AS wrote the manuscript with substantial contributions from all authors.

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An understanding of the natural world and what's in it is a source of not only a great curiosity but great fulfillment.
David Attenborough

1

Introduction

1.1 Research background

The immense variation in life forms across the globe intrigued early naturalists and has inspired research in ecology, biogeography, and evolutionary biology ever since. Spatial variation in diversity was noticed early, especially the most conspicuous pattern, the higher number of species and, more generally, forms, structures, and colours in the tropics compared to temperate regions. This higher diversity was already associated with climatic influences, particularly temperature, by von Humboldt in the early nineteenth century (1808; also see Hawkins 2001). Since then, the question of why some regions hold more species than others has become one of the main challenges in ecological research. Altogether, more than 120 hypotheses have been proposed to explain spatial variation in species richness (Pianka 1966; Rohde 1992; Palmer 1994). These include many hypotheses related to climate, in particular ambient energy, water availability, and productivity, which have been shown to be primary drivers of species richness of many taxa (Currie 1991; Kerr and Packer 1999; Hawkins et al. 2003a,b; Currie et al. 2004; Field et al. 2009). In addition, many other contemporary factors such as area (Arrhenius 1921; MacArthur and Wilson 1963, 1967), biotic interactions and environmental heterogeneity (Simpson 1964; August 1983; Tews et al. 2004; Kissling et al. 2007; Field et al. 2009; Tamme et al. 2010), and disturbance (Petraitis et al. 1989; Huston 1994; Rosenzweig 1995) have been found to be important. Further hypotheses relate to regional or historical factors, such as geological and climatic history, including plate tectonics and glaciations (Pianka 1966; Qian and Ricklefs 2000; Hawkins et al. 2003b; Fine and Ree 2006; Svenning and Skov 2007). Finally, species richness has been thought to be influenced by the mere geometry of regions (Colwell and Lees 2000; Jetz and Rahbek 2001; but see Hawkins et al. 2005). While the impact of some of these factors, such as climate or area, are quite well understood, the role of environmental heterogeneity remains unclear.

The relationship between spatial environmental heterogeneity (EH hereafter) and species diversity has received considerable attention in the literature. A causal relationship between heterogeneity in the physical environment and the diversity of organisms and vegetation zones was already recognised by von Humboldt and Bonpland (1805), von Humboldt (1845) and Spencer (1862), although the latter focused on temporal and evolutionary, rather than spatial, effects. Many subsequent research efforts shaped this general expectation into the more specific heterogeneity hypothesis, according to which areas with higher structural complexity or spatial heterogeneity in environmental conditions harbour more species than homogeneous areas (Pianka 1966; Rosenzweig 1995; Tews et al. 2004). Seminal research by MacArthur and MacArthur (1961) revealed a positive relationship between foliage height diversity, as a measure of vegetation structure, and bird species diversity. This early work motivated many subsequent studies that similarly reported positive associations between vegetation structure and species diversity of birds (MacArthur et al. 1966; Karr 1968; Recher 1969; Karr and Roth 1971; Terborgh 1977), mammals (Rosenzweig and Winakur 1969; August 1983; Kerley 1992) and lizards (Pianka 1967). The close association between area, variability in environmental conditions and habitat types, and species richness was also first addressed early on (Hamilton et al. 1963; Williams 1964; Lack 1969). Since then, numerous studies have reported positive relationships between number or diversity of habitat types and species richness of plants (Deshaye and Morisset 1988; Kohn and Walsh 1994; Hannus and von Numers 2008), birds (Reed 1981; Kitchener 1982; Ricklefs and Lovette 1999), reptiles (Kitchener et al. 1980; Kitchener 1982; Ricklefs and Lovette 1999), mammals (Kitchener 1982; Newmark 1986; Heaney 2001), and various groups of invertebrates (Ricklefs and Lovette 1999; Kerr et al. 2001; Triantis et al. 2005, 2008b). Other studies have used measures of topographical complexity, above all elevation range, as proxies of habitat diversity and have reported positive associations with species richness of various taxa, including mammals (Kerr and Packer 1997; Moreno-Rueda and Pizarro 2007), birds (Hamilton et al. 1964; Ricklefs and Lovette 1999; Rahbek and Graves 2001; Jetz and Rahbek 2002; Moreno-Rueda and Pizarro 2007), reptiles (Losos 1986; Moreno-Rueda and Pizarro 2007), butterflies (Ricklefs and Lovette 1999; Brown and Freitas 2000; Hawkins and Porter 2003), and plants (Hamilton et al. 1963; Ackerman et al. 2007; Kreft and Jetz 2007). While many studies have focused on the terrestrial realm, various aspects of EH have also been found to be important for species diversity in limnic and marine systems. For instance, habitat complexity provided by vegetation, corals, algae, and substrate have been shown to be associated with the diversity of fish (Tonn and Magnuson 1982; Gratwicke and Speight 2005), gastropods (Kohn 1968; Brönmark 1985), crustaceans (Stoner and Lewis III 1985), and mixed invertebrates (Dean and Connell 1987). In addition, abiotic EH in open water has been shown to promote coexistence of species with different habitat requirements (Huston 1994). The investigation of EH across a wide range of study systems has thus shown that EH is generally important in driving spatial patterns of species diversity.

Despite the large amount of research conducted during the last decades, there is still no consensus about the general effect of EH on species richness. This is because the strength of association found between EH and species richness has varied greatly among studies. For instance, MacArthur and MacArthur (1961) found that bird species diversity in deciduous forests was influenced by foliage height diversity, but not by plant species diversity, apart from an indirect effect through vegetation structure. While some authors corroborated these results (e.g. Rosenzweig and Winakur 1969; Kerley 1992), others could not confirm them or questioned their generalisability to other habitat types (Tomoff 1974; Willson 1974; Ralph 1985). Moreover, several later studies found positive relationships between plant species richness and species richness of birds (Power 1972; Harris 1973; Seto et al. 2004), various vertebrates (Kitchener 1982; Qian and Kissling 2010), and insects (Williams 1982; Chown et al. 1998; Kumar et al. 2009). Altogether, positive, negative, hump-shaped, and non-significant EH–species richness relationships have been reported (e.g. August 1983; Monadjem 1999; Marini et al. 2008; Tamme et al. 2010; Allouche et al. 2012; Gazol et al. 2013; Laanisto et al. 2013). The generality of a favourable influence of EH on species richness has therefore been questioned, even though positive EH–richness relationships are generally predicted by ecological theory.

Several mechanisms have been proposed to link EH and species richness. Most are expected to result in positive EH–species richness relationships. These are mainly related to niche theory, in that a larger variety of resources and microsites is thought to allow more species with different ecological requirements and adaptations to coexist (Hutchinson 1959; Klopfer and MacArthur 1960; MacArthur and MacArthur 1961; Currie 1991). For instance, higher plant species richness and more complex vegetation structure are thought to be linked with larger niche space and therefore to promote the coexistence of more species of animals, and to some extent other plants, such as epiphytes (Hietz and Hietz-Seifert 1995; Tews et al. 2004). This is because many animal species depend directly on plants for resources such as food, sites for roosting, mating, nesting, oviposition, overwintering, and foraging, and shelter from predators, parasitoids, and harsh environmental conditions (Lawton 1983; Horváth et al. 2001; Tews et al. 2004; Cousin and Phillips 2008). Even if consumer species are not specialised to particular plant species, they may still prefer certain resource types, determined by plant traits such as fruit size, colour, or presentation mode (Kissling et al. 2007). Topographic EH is also associated positively with niche space, as it is closely related to large- and small-scale variation in abiotic conditions including temperature, precipitation, humidity, wind speed and exposure, solar radiation, evaporation, surface geometry, geochemistry, and soil moisture (Thompson 1978; Huston 1994; Fattorini 2006; Moeslund et al. 2013). Consequently, areas with high topographic EH usually contain many different habitat and microhabitat types and thereby allow species with diverse environmental requirements to coexist (Körner 2000). EH is also expected to have a positive effect on species richness by reducing extinction risk and thereby promoting species persistence. Topographic EH is thought to reduce extinction risk by allowing species range shifts and contractions in response to unfavourable conditions caused by climatic fluctuations and competition (Ricklefs and Lovette 1999; Kallimanis et al. 2010; Särkinen et al. 2012). Vegetation complexity may foster the persistence of animal species by supporting larger animal populations, as more complex vegetation is often associated with larger plants (Lawton 1983). Finally, the heterogeneity hypothesis also has an evolutionary aspect, as EH is thought to promote diversification through isolation and adaptation to diverse environmental conditions (Simpson 1964; Pianka 1966; Kallimanis et al. 2010). Topographic EH is again particularly important in this regard, as the occurrence of isolated valleys and peaks and the associated variation in environmental conditions has promoted speciation in many mountain regions (Jetz and Rahbek 2002; Hughes and Eastwood 2006). For instance, the tropical Andes and African mountains feature exceptionally high numbers of native and endemic species of plants, birds, and mammals (Pomeroy 1993; Hughes and Eastwood 2006; Barthlott et al. 2007; Särkinen et al. 2012). Besides these positive effects of EH on species richness, negative effects have also been suggested. Potential mechanisms behind negative EH–richness relationships include increased extinction risk resulting from fragmentation, habitat loss and isolation (Fahrig et al. 2011; Tews et al. 2004; Kadmon and Allouche 2007; Tamme et al. 2010; Allouche et al. 2012; Laanisto et al. 2013), and higher energy cost of movement through structurally more complex habitats (Lassau and Hochuli 2004). Given this large variety of mechanisms expected to influence EH–richness relationships, it is unsurprising that it has been difficult to reach general conclusions about the effects of EH on species richness.

Another reason why our understanding of the effects of EH on species richness has been limited is the high variability in research approaches. Consistent with the variety of mechanisms expected to underlie EH–species richness relationships, various aspects of EH have been treated separately in the literature. Researchers have investigated the relationships between species richness and many different measures of EH, involving vegetation structure, plant diversity, habitat diversity, topographical complexity, and soil diversity (e.g. Johnson and Simberloff 1974; Fraser 1998; Linder 1991). EH measures have also been computed in many different ways, including simple approaches such as ranges and standard deviations, but also diverse, complex indices, including many based on large-scale environmental datasets such as WorldClim (Hijmans et al. 2005) and remote sensing data (Turner et al. 2003). In addition, the terminology used in EH–richness studies is highly variable and often inconsistent. Studies have also varied greatly in their ecosystems, regions, and taxa of focus. This hampers generalisation because the effects of EH on species richness are known to be highly affected by regional differences (Kerr and Packer 1997; Kreft and Jetz 2007) and taxon-specific characteristics, such as body size, range size, motility, trophic group, and habitat specialisation (Huston 1994; Jetz and Rahbek 2002; Tews et al. 2004). Another complication is scale-dependency, as many measures of EH scale positively with area (Triantis et al. 2003), and different EH–species richness relationships have been reported for different spatial scales (Rahbek and Graves 2001; van Rensburg et al. 2002; Tamme et al. 2010). As it is difficult to draw overall conclusions from such a complex mix of theory, research approaches, and findings, a review of EH–richness studies is urgently needed for further progress in this field.

1.2 Meta-analysis

Review articles have long been a means for synthesising and generalising different studies and have thereby provided useful overviews of various fields. The last decades have shown a steep increase in research exploring EH–species richness relationships, and reviews are thus essential to advancements in this area. However, traditional narrative reviews are subjective, biased and rarely reproducible, as their literature search and interpretative strategies are generally not made transparent (Arnqvist and Wooster 1995; Gates 2002). In addition, the large amounts of data involved in reviews are difficult to handle and interpret, so that particular studies are often arbitrarily overemphasized (Koricheva et al. 2013). As a result, the choice of studies and conclusions derived can differ widely between reviewers, and it is difficult to update or follow up on past reviews. After initial attempts with vote counting techniques, meta-analysis has become established as the standard method for formally and systematically synthesising results from previous studies. Following on its successful establishment in medical and social sciences, meta-analysis is now a widespread and much appreciated tool in ecology and evolutionary biology (Koricheva et al. 2013).

The purpose of meta-analysis is to quantitatively combine the outcomes of different studies, and it aims at answering the following questions (Arnqvist and Wooster 1995): (a) how large is the overall effect under study and does it significantly differ from zero? (b) Which study characteristics influence the variability in magnitude of the effect? The meta-analytical approach involves several formal, methodological steps, details of all of which need to be reported. The initial literature search should be as comprehensive as possible, and all search strategies should be properly described(Gates 2002). Studies should then be selected for inclusion in the final analysis according to clearly specified inclusion criteria. The characteristics of each study are thoroughly extracted, which may easily take up to eight hours for a single study (Wilson 2009). Subsequently, the statistical outcomes of all studies are converted to a common effect size, i.e. a standardised measure of the strength of the relationship of interest. Most commonly, standardised mean differences, response ratios, or correlation coefficients are used as effect sizes, with the choice of effect size measure made based on the characteristics of the underlying data (Harrison 2011). Correlation coefficients, which are commonly used in the ecological literature and therefore in many ecological meta-analyses, are usually transformed to Fisher's z because of its normalizing and variance stabilizing properties (Shadish and Haddock 2009). The next step in meta-analysis is usually the calculation of an overall mean effect size, weighted by sample size so that larger and therefore more reliable studies have a greater influence on the outcome. Random-effects meta-analysis, where study identity is treated as a random effect, additionally makes it possible to generalise inferences beyond the dataset at hand, i.e. to all potential studies (Hedges and Vevea 1998). In a further step, mixed-effects meta-regression allows for investigating the influence of study characteristics on the effect size. All these steps contribute to the reproducibility and comprehensiveness of meta-analysis and enable generalisation and exploration of differences among studies.

Meta-analysis has several advantages over single studies, but also some drawbacks. On one hand, meta-analysis allows both identification of large-scale patterns and investigation of heterogeneity among study outcomes, thereby leading to a deeper understanding of study systems than is possible with single studies. Another clear benefit is that, in contrast to single studies, which often suffer from small sample sizes, meta-analysis reduces type II error rates through increased statistical power and can detect significant effects even when all underlying studies failed to do so (Stewart 2010). On the other hand, meta-analysis has been criticised for mixing apples and oranges (compare e.g. Arnqvist and Wooster 1995), and care must thus be used in the selection of studies, to ensure that they are truly comparable. A further drawback is the high risk of bias in the publication and selection of studies (Gates 2002). In addition, the combination of non-independent effect size estimates in the same analysis can be problematic (Hedges et al. 2010). However, meta-analysis provides means to deal with these drawbacks, e.g. through the investigation of homogeneity among studies, visual and analytical tests for publication bias, robust variance estimation, and sensitivity analyses (e.g. Egger et al. 1997; Gates 2002; Hedges et al. 2010; Stewart 2010). Thus, the advantages of meta-analysis clearly outweigh the potential disadvantages, and the method has great potential to advance scientific knowledge in all research fields. For these reasons, meta-analysis plays a central role in achieving this thesis' aim of gaining a more fundamental understanding of the EH–richness relationship.

1.3 Study outline

The current thesis aims at advancing our understanding of the complex concept of EH and its role in shaping species richness patterns of different taxa worldwide. I first address two closely related sets of research questions: (1) how has EH been quantified and termed in the literature, which mechanisms have been proposed to explain EH–richness associations, and which study systems are most common in EH–richness research (2) What is the actual direction and strength of the EH–richness relationship, and which core determinants influence this association? Building on the foundational insights from these first investigations, I then undertake a global case study exploring differences and similarities among a range of EH measures and comparing their relationships with terrestrial mammal species richness.

The first two research chapters (chapters 2 and 3) are closely related, as they are based on the same dataset. This is derived from a comprehensive, formal search of the EH–species richness literature, involving multiple search strategies and resulting in a final dataset of 1148 data points from 192 studies.

In chapter 2, I survey EH measures and terms and develop a classification of measures based on subject area, e.g. vegetation or topography, and calculation method. I investigate whether a consensus exists with respect to the meaning of EH terms, such as habitat diversity or complexity, and their combination with quantification methods. I also review trends in the EH–richness literature regarding geographic region, habitat type, study taxon and methodology, and thereby identify research gaps. In addition, I provide an overview of the mechanisms behind positive EH–richness relationships that are discussed in the literature and classify them according to their connection with species coexistence, persistence, and diversification. Finally, I investigate associations between study characteristics, such as the hypothesized mechanism, EH measure of interest, and the study taxon and spatial scale used, to identify patterns and further research bias.

In chapter 3, I conduct a formal meta-analysis to quantify the overall strength and direction of the relationship between EH and species richness of terrestrial plants and animals. As EH is closely related to area, I also examine the impact of considering only studies based on equal-area units. Building on the classification established in chapter 2, I explore variation in the EH–richness relationship between biotic and abiotic EH measures, and among the different EH subject areas. Then, using mixed-effects meta-regressions and data subsets representing specific types of EH measures, I identify the key drivers of differences in the EH–richness relationship among studies. To this end, I investigate the influence of study-specific characteristics, representing study location, taxonomic group, and study methodology, including spatial scale, on these differences.

Finally, I use the insights gained in the literature review to inform a case study comparing a range of EH measures in their spatial patterns and associations with species richness of terrestrial mammals worldwide (chapter 4). First, I calculate 51 EH measures representing five EH subject areas and nine calculation methods. Then, I explore their similarity through correlation and principal component analysis and illustrate regional differences in particular EH measures as well as in multidimensional EH space by plotting them on global maps. Moreover, I scrutinise the relationship between mammal species richness and EH by comparing the model support among EH measures based on single-predictor models and multi-predictor models that additionally account for current climate, biogeographic region, and human influence. Using conditional inference trees, I investigate whether the choice of subject area or calculation method of EH measures has a larger impact on model support. Based on findings from chapter 3 that spatial scale is a vital determinant of EH–richness relationships, I repeat the analysis across three spatial grains. Together, these analyses make up the most comprehensive comparison of EH measures across subject areas and their relationship with species richness yet, and provide an opportunity to test the findings of the meta-analysis in chapter 3.

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2

Terminology and quantification of environmental heterogeneity in species-richness research

2.1 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.

2.2 Introduction

2.2.1 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 and MacArthur 1961), lizards (Pianka 1967), and plants (Hamilton et al. 1963; Johnson and Simberloff 1974) already encompassed various aspects of heterogeneity and structure in the environment. For instance, MacArthur and

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, specialisation, and provision of refugia where populations persist during periods of climate change (Pianka 1966; Cowling and Lombard 2002; Durães and 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 et al. 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.

2.2.2 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 and 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 and Rollo 1991; Wagner et al. 2000). Ettema and 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 et al. (1988) considered habitat heterogeneity to be one aspect of habitat variability, and habitat diversity to be a second aspect. By contrast, Li and 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 2.1). 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 and Snelling 1995; Durães and Loiselle 2004; Ackerman et al. 2007). It can therefore be difficult to determine whether terms used in different studies refer to the same concept or not (McCoy and 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" were missed. In addition to using variable terminology, studies have encompassed various quantifica-

Table 2.1 Glossary of terms related to spatial environmental heterogeneity (EH).

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 et al. 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 et al. 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.

tion 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.

2.2.3 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 latu* (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 2.1). 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 and 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 2.2). 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. 2.1). Furthermore, we refer to the methodological and mathematical approach employed for each measure as its "calculation method" (see Table 2.2 for examples).

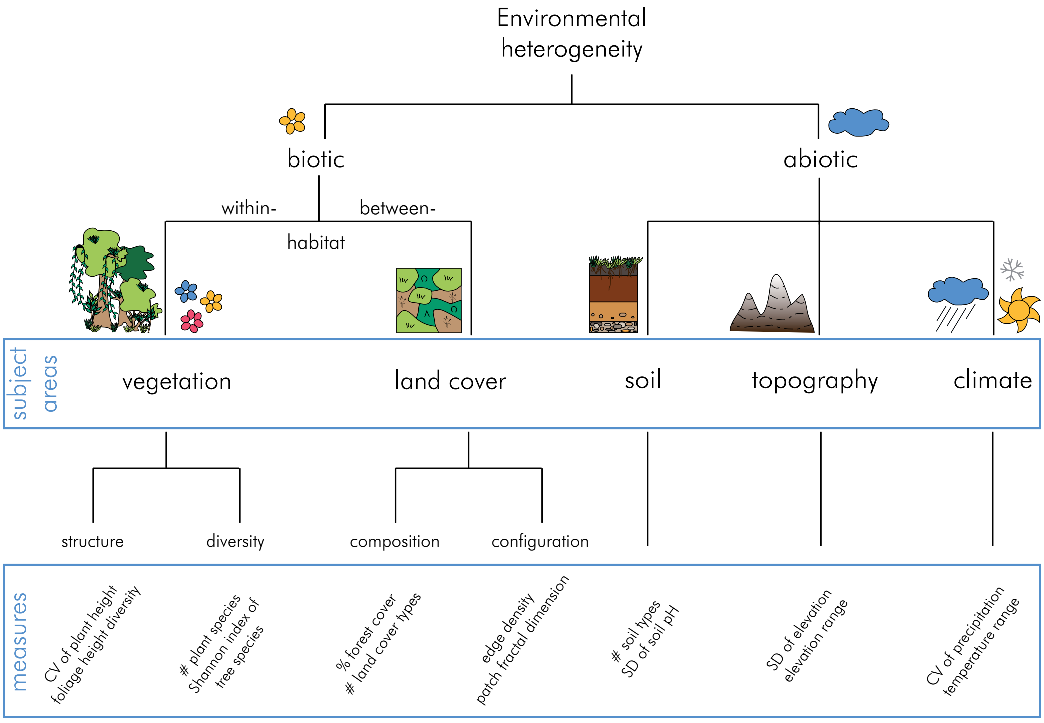

Figure 2.1 Components and quantification of environmental heterogeneity (EH). EH can be differentiated into biotic and abiotic components, which are represented by five subject areas: vegetation (within-habitat component, i.e. vegetation structure and plant diversity), land cover (between-habitat component, 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 2.2).

Table 2.2 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. 2.1). A given term of EH may be quantified by different measures in different studies or even within the same study. Abbreviations: CV, coefficient of variation; #, number of; SD, standard deviation. Ref: exemplary references.

Term	Measure	Calculation method	Subject area	Ref.
Environmental heterogeneity	CV of precipitation	CV	climate	3, 6
	# soil types	count	soil	3, 7
Habitat diversity	# land cover types	count	land cover	2, 12
	elevation range	range	topography	4, 5
Habitat heterogeneity	SD of elevation	SD	topography	8, 15
	elevation range	range	topography	10, 11
Landscape structure	% forest cover	percentage	land cover	1, 13
Structural complexity	foliage height diversity	index	vegetation	9, 14

(1) Danell et al. (1996); (2) Deshaye and Morisset (1988); (3) Durães and Loiselle (2004); (4) Ferrer-Castán and Vetaas (2005); (5) Finch et al. (2008); (6) Fraser (1998); (7) Johnson and Simberloff (1974); (8) Joly and Myers (2001); (9) Karr and Roth (1971); (10) Kerr and Packer (1997); (11) Kissling et al. (2008); (12) Kohn and Walsh (1994); (13) Ma (2008); (14) Orians (1969); (15) Pereira et al. (2007).

Specifically, we addressed the following questions: (1) which terms and measures of environmental heterogeneity have been used, and in which combinations? (2) How can these measures be classified by methodology and subject area? (3) Are there trends in the terminology and quantification of environmental heterogeneity regarding different concepts, methodological approaches, spatial scales, study locations or taxa? (4) 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?

2.3 Review of studies on EH–richness relationships

2.3.1 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 supporting information, Appendix A.1, for details), (2) an inspection of the studies cited in several review articles (Ricklefs and 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 km^2) 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 and 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 Appendix A.2). 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 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 Appendix A.2). Approximately half of the studies were published in the last decade (Fig. 2.2, 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 standardised approach of our literature search and study selection, however, we are confident that we have compiled a representative subset of the relevant literature.

2.3.2 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 2.1). These subject areas represent biotic as well as abiotic components of heterogeneity (Fig. 2.1).

EH–richness relationships are studied from small to large spatial scales. With regard to abiotic EH, this involves, for 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 and 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 and 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 and 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 and 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 and Lovette 1999; van Rensburg et al. 2002). Land cover EH incorporates the composition of cover types as well as their configuration, i.e. the spatial arrangement of elements (McGarigal and Marks 1994; Turner et al. 2001). Due to the predominance of composition measures in our dataset and because measures cannot always be assigned definitely to composition or configuration (McGarigal and Marks 1994), 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 et al. 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 Table A.2).

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 and Harper 1976; also see Brown and Freitas 2000). Due to their rareness in our dataset, we focus on measures that can be assigned to a single subject area.

2.3.3 Quantitative description of studies

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. 2.2), 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 et al. 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).

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. 2.2). 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. 2.3),

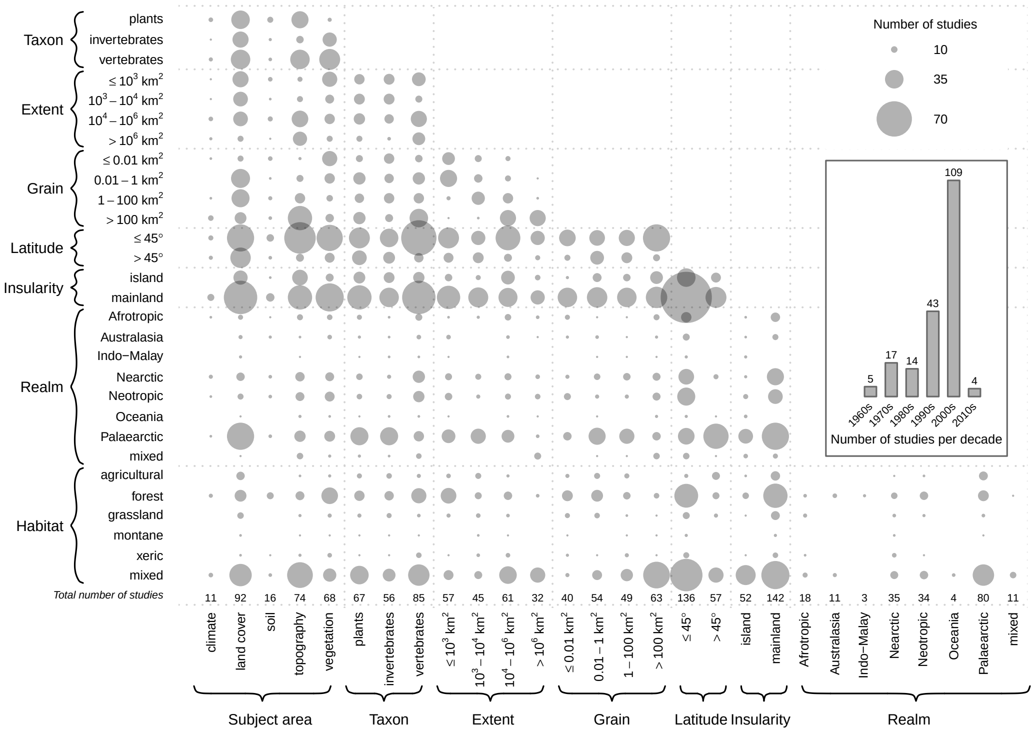

Figure 2.2 Representation of subject areas of environmental heterogeneity (EH), taxonomic groups, spatial extent and grain, latitude (absolute latitude of centroids), insularity, biogeographic realms, and main habitat types in our dataset. Bubble size is proportional to the number of studies analysing 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.

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 et al. 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. 2.3). Again, this bias might be partly due to our selection criteria, as more soil studies may be found at smaller spatial scales, for instance.

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. 2.2). 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 forest systems while focusing only on vegetation EH. Martin et al. (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).

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 km^2, 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% $> 10^4$ km^2, 35.1% $> 10^6$ km^2; Fig. 2.2), while land cover studies focused more on a landscape extent (62.0% $< 10^4$ km^2). 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% $< 10^4$ km^2), whereas studies conducted at continental to global extents mainly considered vertebrate richness (71.9% of the studies conducted at $> 10^6$ km^2).

Our dataset also varied highly in spatial grain sizes, ranging from 1 m^2 plots to 5° grid cells and islands or political provinces of more than 10^5 km^2 area. In small-grain studies, the most frequently analysed group were invertebrates (45.0% of all studies conducted at grains ≤ 0.01 km^2), while vertebrate studies made up 55.6% of the studies conducted at grains >100 km^2. 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. Danell et al. 1996; Currie 1991). Woody plants tended to be studied at larger spatial grains than herbs (largest fraction, i.e. 50.0% of woody plant studies > 100 km^2, 46.7% of herb studies < 1 km^2). This is not

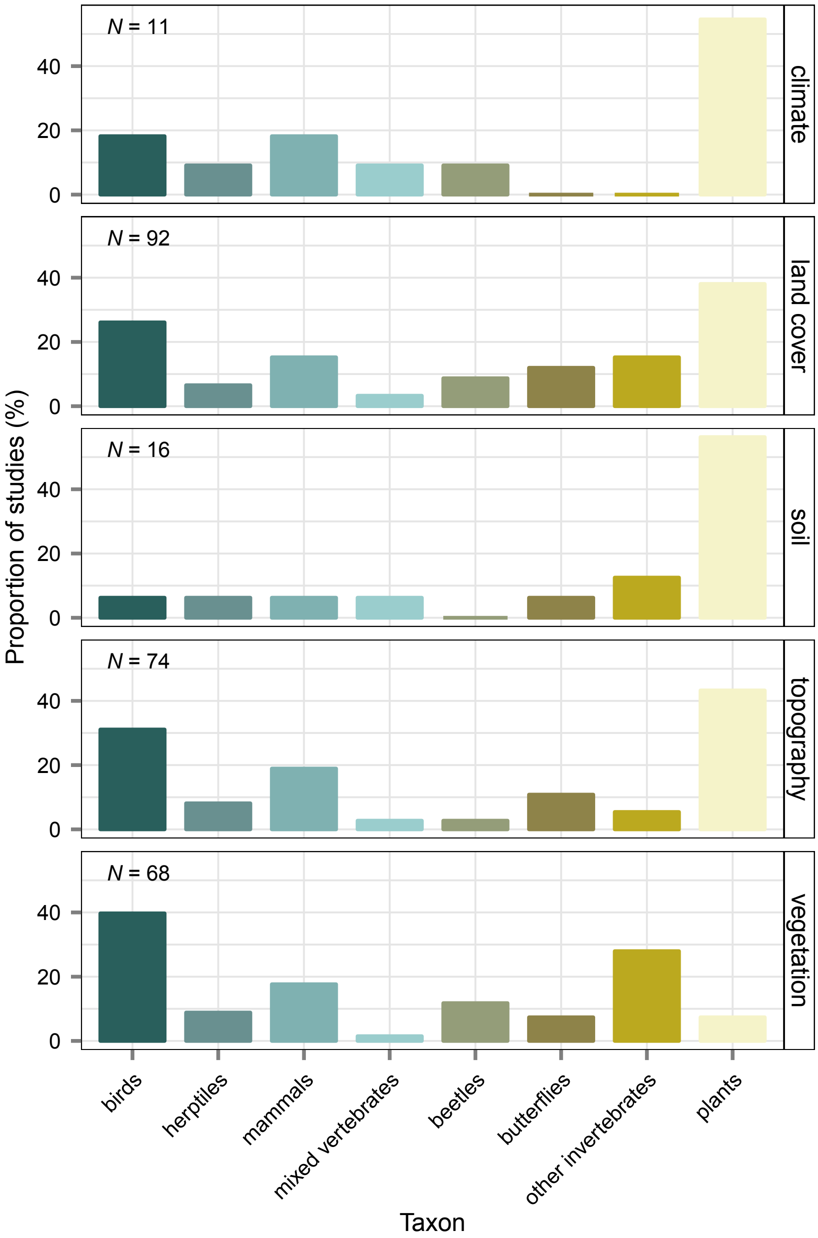

Figure 2.3 Proportion of studies analysing species richness of various taxonomic groups in relation to environmental heterogeneity (EH) distinguished by subject area. The 100% reference level for each panel is N, the total number of studies considering climatic, land cover, soil, topographic, and vegetation EH, respectively.

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.

2.3.4 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 (Fig. 2.4 and Table A.2). The most frequent term for EH was "habitat diversity" (Fig. 2.4), which occurred (linked to a measure) in 59 studies. Forty-two studies dealt with "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 and Marks 1994; 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 et al. 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).

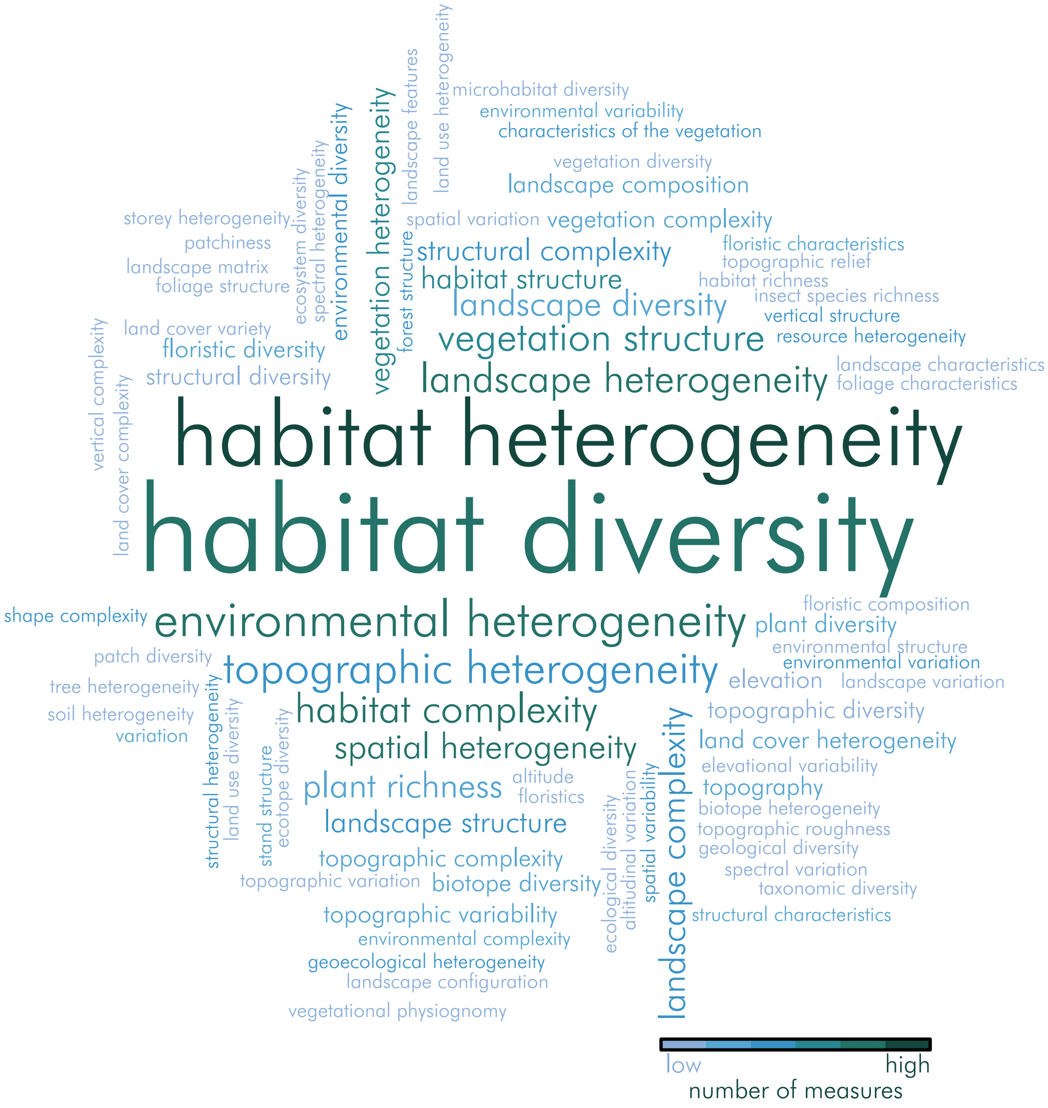

Figure 2.4 Terms for EH used in our dataset that could be associated with a measure in at least one study. Font size is proportional to the number of studies using each term. Colour ramp signifies the number of measures used to quantify each term (six classes: 1–2, 3–5, 6–9, 10–19, 20–29, 42 measures).

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 and 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.

2.3.5 Quantification of EH

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 (Table A.2). 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 Table A.2), 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. 2.4).

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 generalise 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 and 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 standardised 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).

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 (Figs. 2.5 and A.1), 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 and Medellín 2001) and therefore represent the most variable calculation method. By contrast, only 4.8% of all measures 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; Fig. A.1). 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 and Marks 1994; 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 and 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 (Fig. A.2). 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. 2.5). 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. 2.5). 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. 2.5) 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 ($\leq 10^4$ 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 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 (≤ 1 km^2), whereas range measures were mostly used at larger spatial grains (71.0% > 100 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. 2.6). 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 of studies applying each method fluctuated over the past decades (Fig. A.3). 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.

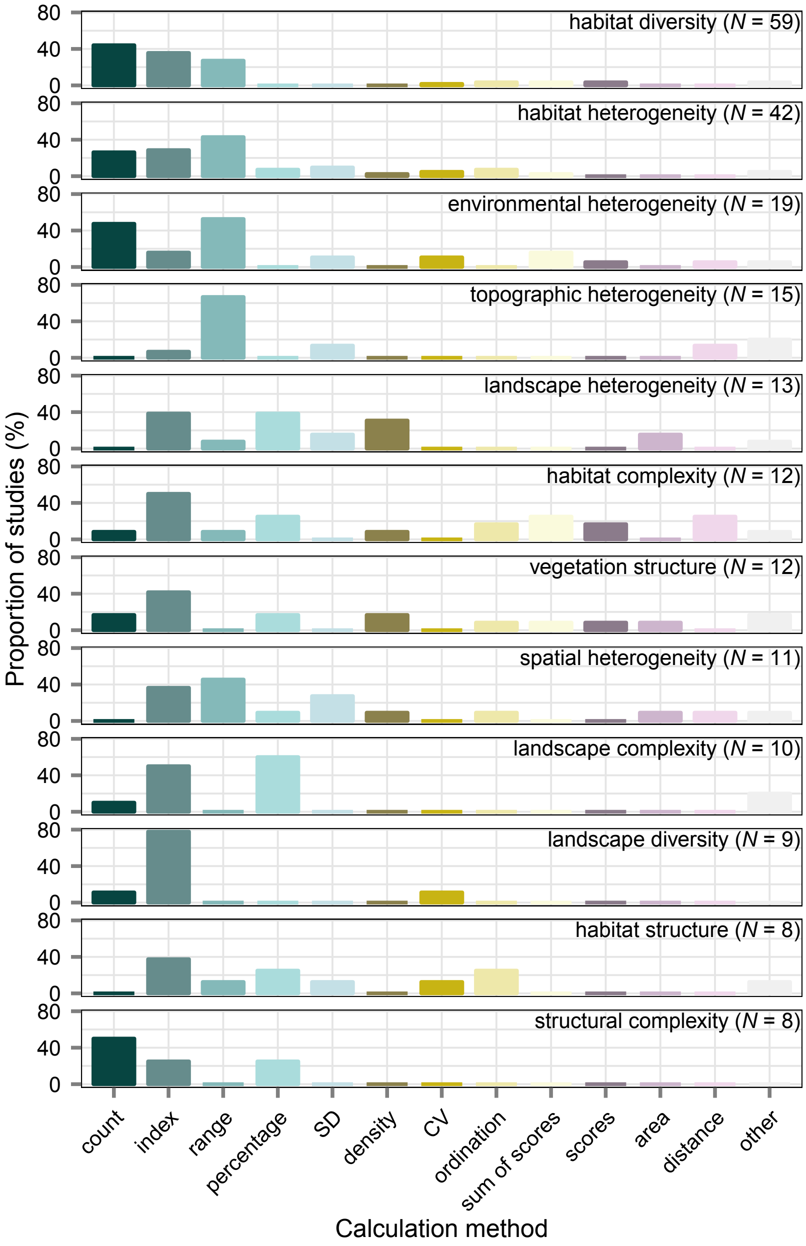

Figure 2.5 Proportion of studies using different calculation methods for the quantification of environmental heterogeneity (EH) in combination with a given term for EH. Only the most common terms are displayed in the order of their frequency. The term "plant richness" (N = 9) only occurred in combination 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.

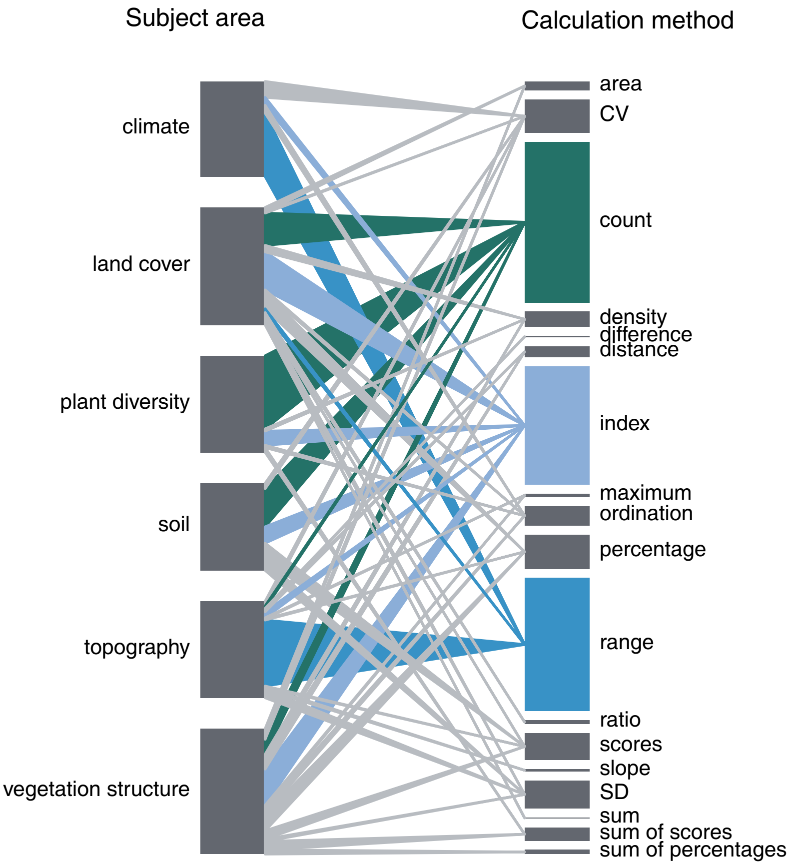

Figure 2.6 Occurrence of calculation methods in environmental heterogeneity (EH) measures according to subject area. Plant diversity and vegetation structure are treated as separate subject areas to show the differences in calculation methods. Line width is proportional to the number of studies applying 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.

2.3.6 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 and 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 and 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 (a) species coexistence, (b) species persistence, and (c) species diversification (Table 2.3). 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 and Whittaker 2002). At a landscape scale, land cover, soil, or topographic EH may affect species turnover at the scale of centuries to millennia (Willis and 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 et al. 2003; Tamme et al. 2010). Furthermore, species richness of habitat specialists may be linked more closely to EH than that of habitat generalists (Ricklefs and 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 and 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 et al. 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.

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 2.3). 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 et al. 1998; Novotny et al. 2006; Kumar et al. 2009), birds (Seto et al. 2004), and vertebrates (Qian and 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 et al. 2007, 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 et al. 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 and Fernandes 2001). Accordingly, the largest portion of studies referring to the presented mechanisms analysed vegetation EH, followed by land cover EH (Table 2.3).

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. Deshaye and Morisset 1988; Homeier et al. 2010; Table 2.3). 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 and Hawkins 2008).

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

Table 2.3 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. The given numbers 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.

	Mechanism	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	veg 43, lan 37, top 34, soi 9, cli 6	ver 40, pla 9, inv 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)	lan 5, top 5, soi 2, cli 1	pla 6, ver 4, inv 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	lan 10, veg 10, soi 2, top 1	inv 12, ver 5, pla 1	forest 7, agricultural 5, mixed 4, grassland 1	△
	reduced extinction risk through reduced competitive pressure	veg 3, top 2, lan 1	ver 3, pla 2, inv 2	mixed 3, forest 1, grassland 1	
	survival of populations through vertical range shifts and refuges in periods of adverse environmental conditions	top 8, lan 3, soi 2, cli 1, veg 1	pla 4, ver 4, inv 2	mixed 7, forest 1, xeric 1	
diversification	divergent natural selection, specialisation and adaptive radiation through diverse environmental pressures and opportunities	top 5, lan 3, soi 2, veg 2, cli 1	pla 3, ver 3, inv 2	mixed 5, forest 2	△
	allopatric speciation through isolation of populations by physically or physiologically effective barriers	top 7, veg 3, soi 2, cli 1, lan 1	pla 4, ver 4, inv 1	mixed 6, forest 2	

cli, climate; lan, land cover; soi, soil; top, topography; veg, vegetation; inv, invertebrates; pla, plants; ver, vertebrates.

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 and Hochuli 2005; Garden et al. 2010; Table 2.3). 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 and 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 and 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 and Lovette 1999).

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 and 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 and O'Brien 2000; Durães and Loiselle 2004). These studies mostly investigated topographic EH at spatial grains > 100 km^2 (Table 2.3). 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 and 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 and Eastwood 2006), and the region is paramount in the number of native and endemic species of plants and vertebrates (Hughes and 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 specialisation and adaptive radiation through a wider variety of environmental pressures and opportunities (e.g. Kallimanis et al. 2010; Table 2.3). 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 et al. 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.

2.3.7 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. 2003a). 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 and 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 and Walsh 1994; Ricklefs and Lovette 1999; Triantis et al. 2003, 2005; Hannus and von Numers 2008). Area is expected to influence species diversity through effects on immigration, extinction, and speciation rates (MacArthur and Wilson 1963, 1967; Kisel et al. 2011) or via an increase of EH (Williams 1964; Johnson and 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 and 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 and Lovette 1999). Also topography correlates not only with heterogeneity in environmental conditions but also with surface area (Ferrer-Castán and Vetaas 2005). Triantis et al. (2008a), 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 and 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 and 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 et al. 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 et al. 2001).

2.4 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. (a) 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. (b) 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. (c) 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. (d) 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 reanalysis of existing datasets evaluating multiple standardised 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 generalise, 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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3

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

3.1 Abstract

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

3.2 Introduction

A major goal in ecology is to understand spatial patterns in the distribution of species diversity. Among the most important factors governing diversity gradients are contemporary factors such as ambient energy, water availability and productivity, area, biotic interactions and environmental heterogeneity, and factors related to historical processes such as phylogenetic niche conservatism and geological or climatic history (Currie 1991; Hawkins et al. 2003a; Kreft and Jetz 2007; Field et al. 2009). In addition, a role of geometric constraints in shaping diversity gradients has been discussed (Colwell and Lees 2000). Spatial environmental heterogeneity (EH) is thought to promote species diversity through three major mechanisms: First, an increase in environmental gradients and in the amount of habitat types, resources and structural complexity should increase the available niche space and thus allow more species to coexist (e.g. Currie 1991; Tews et al. 2004). Second, environmentally heterogeneous areas are more likely to provide shelter and refuges from adverse environmental conditions and periods of climate change, which in turn should promote species persistence (e.g. Seto et al. 2004; Kallimanis et al. 2010; Fjeldså et al. 2012). Third, the probability of speciation events resulting from isolation or adaptation to diverse environmental conditions should increase with higher EH (e.g. Rosenzweig 1995; Hughes and Eastwood 2006; Antonelli and Sanmartín 2011).

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

The role of EH in shaping richness patterns is particularly prone to controversy because of the high variability in research approaches and terminology, which may obscure the importance of EH in some study systems and impede generalisations from single studies (compare Box 3.1). EH incorporates heterogeneity in both biotic and abiotic conditions, which we classify into five subject areas: land cover and vegetation on one hand, and climate, soil and topography on the other hand (Box 3.1). Despite varying concepts and quantification methods, EH is assumed to have a positive effect on richness, underlain by similar mechanisms, across studies and subject areas.

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

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

Regarding the third question, our analysis was guided by the following hypotheses: (1) The importance of different components of EH differs among taxa. For instance, species richness of taxa depending directly on plants as resources should be affected more strongly by vegetation EH than by abiotic EH components, particularly at smaller spatial scales (Tews et al. 2004). Plant diversity should be particularly important for specialised herbivore richness (De Araújo 2013). (2) The effect of EH is stronger in regions with higher energy availability, where energy is not a limiting factor of species richness (Kerr and Packer 1997; Kreft and Jetz 2007). (3) The EH–richness relationship is scale dependent. The effect of EH should increase with spatial grain, because larger sampling units generally include greater variability in environmental conditions (van Rensburg et al. 2002; Kallimanis et al. 2008). Moreover, EH should be more important at landscape scales, whereas climate and factors related to colonisation and extinction should dominate at large spatial extents (Rowe 2009; Qian and Kissling 2010). (4) Studies conducted using grain sizes of unequal area overestimate the influence of EH due to the confounding effect of area, as area and EH are often closely related (Rosenzweig 1995; Triantis et al. 2003).

Box 3.1 Terminology and quantification of spatial environmental heterogeneity (EH)

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

Similar to the often inconsistent and confusing terminology, quantification of EH has been very diverse, not least because of the high variability in study systems, spatial scales and study taxa. The most frequently used measures for EH include elevation range, number or diversity of land cover types and number of plant species. But also these measures have many synonyms in the literature, impeding the finding of studies, understanding and synthesis. Furthermore, different measures may describe equivalent concepts in different studies, thereby making generalisations difficult: for instance, diversity in biotope, ecosystem, or habitat types relate to similar concepts, and the number of bird-dispersed vs. caterpillar food plant species both refer to food plant richness (e.g. Hawkins and Porter 2003; Kissling et al. 2007). We classified EH measures into five subject areas (compare Table 3.1):

Biotic EH

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

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

Abiotic EH

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

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

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

3.3 Methods

3.3.1 Study selection

We systematically searched the literature for studies investigating the relationship between one or more measures of EH and species richness. We applied three different approaches to detect as many studies as possible and reduce bias in data selection. First, we used the topic search in *ISI Web of Science*, including all years until April 2011, all languages and all document types. Our extensive search string contained 68 different terms for EH, such as 'habitat diversity', 'landscape complexity' and 'topograph* heterogeneity', in combination with '"species diversity" OR "species richness" OR "species number" OR "species density"'(see Appendix B.1 for details and full search strings). Second, we screened the references included in several relevant reviews (Ricklefs and Lovette 1999; Tews et al. 2004; Field et al. 2009; Hortal et al. 2009; Lundholm 2009; Tamme et al. 2010). Third, we inspected the references cited by the articles found through the first two search modes.

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

3.3.2 Data extraction

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

We recorded the following study characteristics, if available: (1) taxon: taxonomic group, trophic group, thermoregulation; (2) location: geographic coordinates, biogeographic realm and biome according to Olson et al. (2001), insularity, main habitat type; (3) methodology: whether the units of analysis were of equal area or not, spatial grain and extent, sample size (e.g. number of plots), EH measure and subject area. We classified measures within subject areas into EH measure categories so that they related to the same concept (Table 3.1). Many studies reported multiple EH–richness relationships, which we recorded as separate data points within each study. These were based on multiple study locations, taxa, spatial scales or EH measures.

If the information provided on study location and spatial scale was insufficient and could not be obtained from authors, we estimated study location coordinates and study areas using maps, other studies conducted at the same location, or study descriptions. We created spatial polygons for all data

Table 3.1 Subject areas of environmental heterogeneity (EH) categorised into EH measure categories relating to the same concepts with example measures used for quantification of EH.

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

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

Table 3.2 Study characteristics included as covariates in meta-regressions.

Variable	Type	Details
Equal area	cat	0 (109/434); 1 (85/714)
Spatial grain	con	$\leq$ 0.01 km^2 (40/151); > 0.01 km^2 – 1 km^2 (54/254); > 1 km^2 – 100 km^2 (49/391); > 100 km^2 (63/352)
Spatial extent	cat	$\leq$ 1,000 km^2 (57/235); > 1,000 km^2 – 10,000 km^2 (45/327); > 10,000 km^2 – 1,000,000 km^2 (61/424); > 1,000,000 km^2 (32/160)
EH subject area	cat	land cover (92/517); vegetation (68/315); climate (11/56); soil (16/37); topography (74/212); mixed (3/11)
EH measure category	cat	land cover diversity (79/285); land cover proportion (19/108); patchiness (10/124); plant diversity (37/148); vegetation complexity (29/100); vegetation dimension (16/67); climate (11/56); soil diversity (10/25); soil variables (7/12); elevation diversity (67/178); microtopography (5/5); profile (7/29); mixed (3/11)
Habitat type	cat	forest (57/367); non-forest (46/306); mixed (91/475)
Island	cat	0 (142/956); 1 (52/192)
Mean PET	con	mm/a; no transformation
Broad taxon	cat	plants (67/336); invertebrates (56/289); vertebrates (85/523)
Fine taxon	cat	plants (67/336); invertebrates (56/289); birds (54/284); herptiles (13/36); mammals (29/109); mixed vertebrates (3/94)

Details present factor levels of categorical (cat) variables with the according number of studies/data points in parentheses, and units and potential transformations for continuous (con) variables. Categories for equal area and island mean "no" (0) and "yes" (1). For a more comprehensive quantification of study characteristics, see Appendix B.6.

points, using minimum convex hulls to estimate missing spatial extents and centroids of the study areas. We calculated mean potential evapotranspiration (PET) for all study areas based on these polygons and the Global-PET Database (Zomer et al. 2008; http://www.cgiar-csi.org). We recorded spatial grain for all data points as the mean area of the units of analysis. All these study characteristics were used as covariates in the analysis except for thermoregulation, geographic coordinates and biogeographic realm and biome (see Table 3.2 for details). Geographical analyses were performed in ESRI ArcMap and R, packages *maptools* and *rgdal* (ESRI 2010; R Core Team 2013; Bivand and Lewin-Koh 2013; Bivand et al. 2013, respectively).

3.3.3 Statistical analysis

We used Fisher's z to quantify the effect size of EH–richness relationships. We derived z from correlation coefficient r using Fisher's r-to-z transformation (Shadish and Haddock 2009): $z = 0.5 \times \ln[(1 + r)/(1 - r)]$. This transformation is normalising and variance stabilising so that the variance v_z depends only on sample size n and not on the strength of the correlation itself (Shadish and Haddock 2009): $v_z = 1/(n - 3)$. We derived z-values from r^2 values of simple regressions or from F- and t-statistics following Rosenberg (2005). As we were interested only in the simple relationship between EH and species richness, we did not include results from multiple regressions or partial correlations, where coefficients are affected by additional covariates, leading to poor comparability across studies. We changed the sign of effect size estimates derived from EH measures where a higher value signified lower EH, e.g. percentage grassland cover.

The studies varied widely in their design, and we could not investigate the influence of all possible study characteristics on the EH–richness relationship. We therefore used a random-effects framework, where each study-specific true effect is subject to random variation (Viechtbauer 2007). This incorporation of between-study heterogeneity allows for generalisation to all potential studies (Hedges and Vevea 1998). Many studies reported multiple outcomes that were nonindependent, as a result of phylogenetic relatedness of species, spatial autocorrelation or nestedness, multiple measurements on the same community, or specific methods applied by a particular research team (compare Nakagawa and Santos 2012; Mengersen et al. 2013). Ignoring such dependencies would lead to an underestimation of standard errors, impaired statistical inference and a stronger weighting of studies that provide more outcomes (Borenstein et al. 2009). To our knowledge, our study is the first in ecology to use a recent method for robust variance estimation (RVE), which allows for meta-regression with dependent effect size estimates and thereby the utilisation of all available study outcomes (Hedges et al. 2010).

To increase precision of summary effects, we weighted effect size estimates by their inverse variances, such that studies with higher sample sizes were given more weight (Borenstein et al. 2009). We used random-effects inverse variance weights as suggested by Hedges et al. (2010), where the total weight of any single study is bounded so that studies are not assigned more weight just because they provide more outcomes: $w_{ij} = 1/[k_j(v_{\bullet j} + \tau^2)]$; w_{ij}: weight of the i^{th} effect size estimate in the j^{th} study; k_{j}: number of effect size estimates in the j^{th} study; $v_{\bullet j}$: unweighted average of the variances of effect size estimates in the j^{th} study; τ^2: estimate of the between-study variance component. We used a value of 0.8 for the within-study correlation ρ, i.e. the mean correlation between all effect size estimates per study, to estimate τ^2. Sensitivity analyses indicated that our results are robust to variation in ρ (Appendix B.2; compare Hedges et al. 2010). We performed seven separate meta-regression analyses to study overall mean effects, compare different effects for biotic vs. abiotic EH, EH subject areas and measure categories and to test our hypotheses using three different subgroups of the data. Based on an intercept-only model, we first estimated a weighted mean effect size with robust 95% confidence interval (CI; Hedges et al. 2010) for the complete data set. As we expected a significant influence of whether studies were based on equal-area units or not, we also estimated a weighted mean effect size for equal-area studies only. To test whether the strength of the EH–richness relationship differed between EH components, we ran three mixed-effects meta-regressions including biotic vs. abiotic EH, EH subject area or EH measure category as fixed effects. Differences between fixed-effect categories were determined using t-tests on meta-regression coefficients while changing the reference category level. Studies that used composite measures relating to more than one EH subject area (e.g. Harner and Harper 1976) were excluded from these meta-regressions. We also conducted the metaregression with EH measure categories for equal-area studies only.

We tested our hypotheses further using three subgroups of the data, containing related EH measure categories or specific taxonomic groups. EH measure categories that were represented by < 20 studies were omitted (compare Tanner-Smith and Tipton 2014; López-López et al. 2014). Subgroup I contained the EH measure categories elevation diversity and land cover diversity, which are often used as proxies for the number and diversity of habitat types (but see Hortal et al. 2013). Subgroup II included the EH measure categories vegetation complexity and plant diversity. For these two subgroups, we examined multiple covariates simultaneously to account for correlations among covariates and thereby avoid confounding effects (Viechtbauer 2007). Hence, similar to other meta-analyses that have used RVE (e.g. Tanner-Smith et al. 2013), we ran three consecutive meta-regressions. Model 1 tested whether methodological study characteristics affected the average effect size estimate. As spatial scale has often been shown to influence effect sizes (Chase and Knight 2013), we included spatial grain, extent and equal area in this model. Furthermore, we included EH measure category to account for differences in EH measurement. Model 2 tested the effect of the location-related covariates habitat type, mean PET and insularity, while accounting for study methodology. Model 3, the full model, tested the effect of taxon-related covariates, including either broad or fine taxonomic group, while also accounting for study methodology and location. Due to collinearity among covariates, we did not include insularity in the models of subgroup I or mean PET in the models of subgroup II (Appendix B.3). As most studies analysed the effect of vegetation EH on animal richness, we excluded four data points examining the effect of EH on plant richness from subgroup II to allow for a meaningful test of taxonomic group. In models of subgroup I, we excluded two data points for which spatial extent was not available. We included all covariates as study-level means to allow the estimation of between-study effects. Subgroup I included 22 studies that each varied in spatial grain, so we additionally centred spatial grain around the study-level mean to test for within-study effects (Tanner-Smith and Tipton 2014).

We did not include trophic group in these meta-regressions due to collinearity among covariates and because many studies examined taxa that contained multiple trophic groups, hampering interpretation. Therefore, we ran an additional meta-regression on subgroup III to test hypothesis (1). Subgroup III contained only data points on herbivores (including frugivores) and was regressed against EH subject area as a fixed effect. Studies with climatic and soil EH were excluded due to low sample size. We split vegetation EH into vegetation structure and plant diversity, as we expected a stronger link of herbivores to plant diversity.

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

3.3.4 Publication bias

Publication bias arising from the preferential publication of statistically significant, positive and strong effects may impair meta-analytic conclusions (Møller and Jennions 2001). To test whether our results were affected by publication bias, we used funnel plots and Egger's regression test, by including standard error as a covariate in meta-regressions of the complete data set, equal-area studies only and subgroups I–III (Egger et al. 1997; Peters et al. 2008; Viechtbauer 2010). In case of funnel plot asymmetry, we ran additional regression tests using residuals of mixed-effects models to test for publication bias after controlling for heterogeneity (Egger et al. 1997; Nakagawa and Santos 2012). In addition, we calculated Rosenberg's fail-safe number N for the complete data set as an indication of how many studies averaging null results would need to be added to render the overall mean effect size estimate non-significant (Rosenberg 2005; Jennions et al. 2013). We estimated N using study-level mean effect size estimates based on a fixed-effects model with the R package *metafor* (Viechtbauer 2010).

3.4 Results

We compiled 1148 data points from 192 studies (Appendices B.4 and B.5). These included 190 scientific articles published in 71 journals between 1964 and 2011, one conference contribution and one thesis. The study areas covered all continents and biogeographic realms except Antarctica, with a strong bias towards the Palearctic (80 studies; Fig. 3.1, Appendix B.6; note that one study may contain multiple

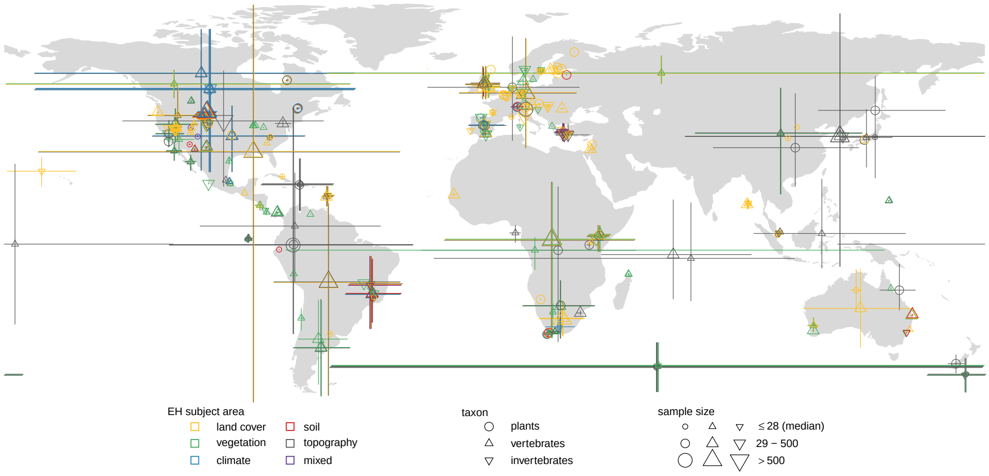

Figure 3.1 Locations of 192 studies contributing a total of 1148 data points to the meta-analysis of EH–richness relationships, distinguished by EH subject area (colour), taxonomic group (symbol) and sample size (symbol size). Symbols mark study location centroids and lines represent latitudinal and longitudinal extents of study locations; three data points with global extent are not shown. Overlapping symbols and lines are slightly offset for clarity.

study locations, taxa, spatial scales, or EH measures). Studies involved both mainland (142 studies) and island systems (52) and most often covered multiple habitat types (91) or focused on forest systems (57). Temperate forests (46 studies) and Mediterranean forests (24) were best represented, whereas studies from taiga (4), montane grassland (2) and tundra (1) biomes were scarce. Invertebrates (56 studies) were relatively underrepresented compared to vertebrates (85) and plants (67). Spatial grain ranged from 1 m^2 plots to 5° grid cells to provinces or islands of more than 10^5 km^2*; spatial extent ranged from 10 km^2 to global. Most studies analysed EH in land cover (92 studies), topography (74) and vegetation (68), while few studies considered climatic (11) or soil EH (16; see Appendix B.6 for more details).

Among the 1148 data points, 1012 showed positive and 134 showed negative EH–richness relationships, 758 and 59 of which, respectively, were statistically significant at $\alpha = 0.05$. Two outcomes were reported as correlations of 0.00. Effect size estimates varied between −1.46 and 2.44, but the overall weighted mean effect size estimate was significantly positive with $z = 0.63$ (95% CI ±0.07; Fig. 3.2). The weighted mean effect size estimate of equal-area studies only was also distinctly positive, but lower with $z = 0.47$ (±0.09).

Meta-regressions assessing the effects of biotic vs. abiotic EH, EH subject area and measure category were performed without intercept; model coefficients can thus be interpreted as average effect size estimates (between-study effects; Figs. 3.3 and 3.4). Coefficients for biotic vs. abiotic EH were close to the overall weighted mean and did not differ significantly from each other (0.63 ±0.10 vs. 0.60 ±0.10; Fig. 3.3). Coefficients for all five EH subject areas were also significantly positive, ranging from 0.34 (±0.27) for climatic EH to 0.67 for topographic (±0.13) and vegetation EH (±0.17; soil: 0.43 ±0.29; land cover EH: 0.61 ±0.12; Fig. 3.3). Average effect size estimates for topographic and vegetation EH were significantly larger than that for climatic EH (topographic EH: $t = 2.04$, $P = 0.04$; vegetation: $t = 2.08$, $P = 0.04$). Land cover EH had a larger average effect size estimate than climatic EH, but this difference was

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*corrected from 10^{11} km^2 in the published version

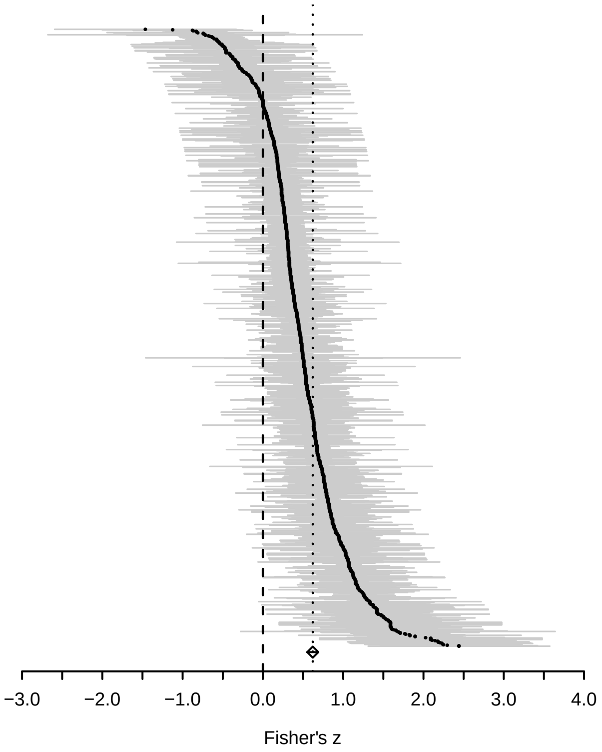

Figure 3.2 Forest plot showing 1148 effect size estimates of EH–richness relationships (black dots) with 95% confidence intervals (CI; grey lines). Black diamond and dotted line represent the overall weighted mean effect size estimate with 95% CI (diamond width); dashed line: zero effect.)

not statistically significant (t = 1.78, P = 0.08). Subject area coefficients were not significantly different otherwise.

In the meta-regression with EH measure categories, average effect size estimates varied between 0.20 (±0.47) for patchiness and 1.35 (±0.81) for microtopography (Fig. 3.4). All coefficients except those for patchiness and soil variables were significantly positive. As in the results for overall mean effect size, coefficients for equal-area studies tended to be slightly smaller than coefficients for the complete data set (Fig. 3.4). Average effect size estimates for soil diversity and vegetation dimension were non-significant when investigating equal-area studies only.

We found stronger effects of covariates in multiple metaregressions of subgroup I than of subgroup II. For subgroup I (considering only the EH measure categories elevation and land cover diversity), all covariates related to spatial scale were significantly associated with average effect size, whereas EH measure category showed no effect (model 1, Table 3.3a, Appendix B.7). Studies that analysed equal-area units showed smaller effects on average than studies that did not keep area constant. Studies using larger spatial grains found stronger positive associations on average between EH and species richness. This was true both for between- and within-study effects. The opposite was true for spatial extent—larger extents were associated with smaller effect size estimates. These relationships all remained statistically significant when location- and taxon-related covariates were added (models 2 and 3). We found no influence of mean PET (model 2). Studies covering multiple habitat types found larger effect sizes on average than studies in forest systems. We found no significant difference between studies in non-forest systems and in forest systems. Taxonomic group did not influence average effect size estimates, whether fine or broad taxonomic groups were included (model 3; Appendix B.8). For subgroup II (considering only the EH measure categories vegetation complexity and plant diversity), we found no significant influence of any included covariates except spatial grain (models 1 and 2; Table 3.3b). As with subgroup I, studies conducted at larger spatial grains were, on average, associated with larger effect size estimates.

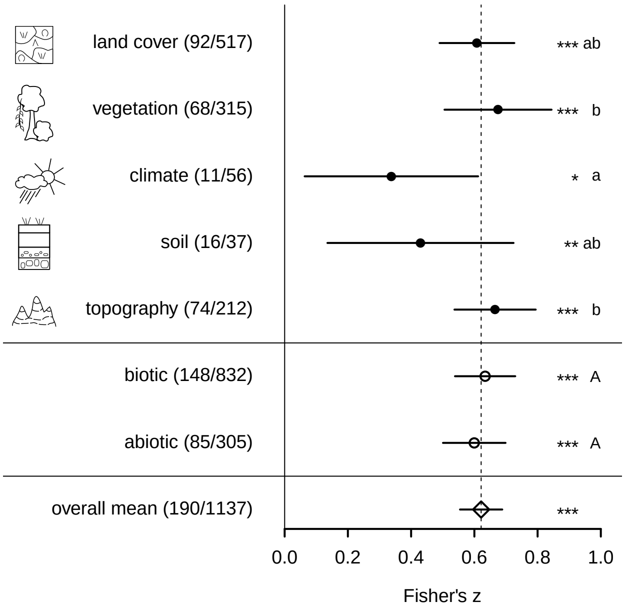

Figure 3.3 Mean effect size estimates for the five EH subject areas and for biotic vs. abiotic EH derived from two separate mixed-effects meta-regressions. Closed and open circles represent coefficients for EH subject areas and biotic vs. abiotic EH, respectively; lines show 95% confidence intervals (CI). Letters indicate significant differences among EH subject areas (lower case) and among biotic vs. abiotic EH (upper case). Diamond and dashed line represent the overall weighted mean effect with 95% CI; 11 data points mixing EH subject areas are excluded. Numbers in parentheses give the respective numbers of studies/data points; note that one study can include multiple EH subject areas and both biotic and abiotic EH. All coefficients are different from zero at significance levels: *** 0.001, ** 0.01, * 0.05.

However, when both location- and taxonrelated covariates were included in model 3, this relationship became non-significant (t = 1.83, P = 0.07).

The meta-regression for subgroup III (herbivores only) revealed that studies analysing land cover or topographic EH had significantly smaller effect size estimates on average than studies analysing plant diversity as a measure of EH (Table 3.4). Effect size estimates of studies analysing plant diversity did not differ significantly from those of studies analysing vegetation structure, although the latter tended to be smaller.

Considering publication bias, almost one third of the included data points did not have statistically significant EH–richness relationships. Still, our study included a relatively high number of data points with large sample sizes and small standard errors (Fig. B.2). Using regression tests, we detected funnel plot asymmetry for the complete data set and for subgroup I (Appendix B.9). However, no asymmetry was found in funnel plots based on mixed-effects model residuals of subgroup I or on effect size estimates of equal-area studies only. Rosenberg's fail-safe number indicated that 211 470 studies with an average effect size of zero would need to be added to render the overall weighted mean (0.41 for a fixed-effects model of study-level mean effect size estimates) non-significant at α = 0.05.

3.5 Discussion

Our meta-analysis of 1148 data points worldwide indicates that EH and species richness are on average positively related across taxa, regions and EH subject areas at landscape to global extents. This positive relationship can be attributed to various mechanisms involved in the promotion of species coexistence, persistence and diversification. Several studies also reported negative EH–richness relationships or

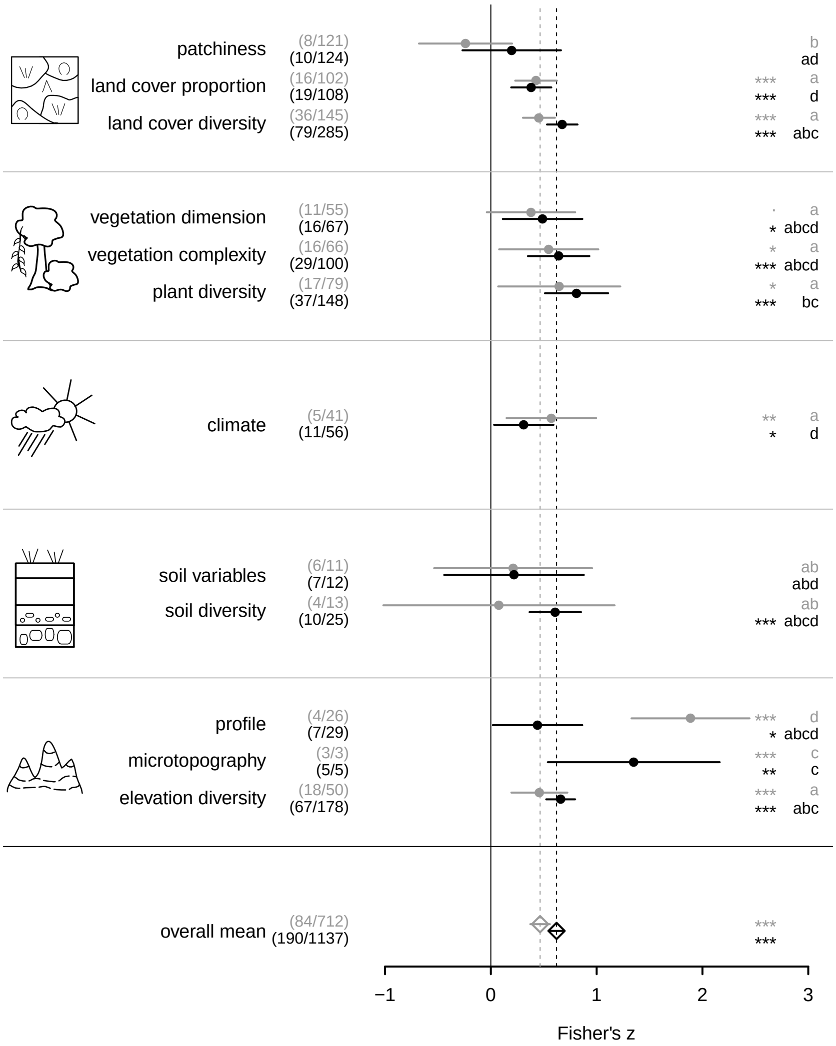

Figure 3.4 Mean effect size estimates of EH measure categories derived from mixed-effects meta-regressions considering either all or only equal-area studies. Black symbols refer to results for all studies, grey symbols to results for studies using equal-area units. Dots and lines represent coefficients with 95% confidence intervals (CI). Letters show significant differences among EH measure categories. Diamonds and dashed lines represent the overall weighted mean effects; 11 data points mixing EH measure categories are excluded. Numbers in parentheses give the respective numbers of studies/data points; note that one study can include multiple EH measure categories. Estimates for microtopography (equal area) not shown for clarity (8.3 ±2.6). Significance levels indicating difference from zero: *** 0.001, ** 0.01, * 0.05.

Table 3.3 Results of mixed-effects meta-regressions for subgroups representing different EH concepts: subgroup I: EH measure categories elevation diversity and land cover diversity (126/461 studies/data points); subgroup II: plant diversity and vegetation complexity (60/244 studies/data points).

	Model 1			Model 2			Model 3		
	b	SE	CI	b	SE	CI	b	SE	CI
(a) Subgroup I									
Intercept	.77***	.15	±.40	.71***	.21	±.54	.73***	.21	±.56
Equal area	−.36***	.08	±.21	−.36***	.08	±.21	−.37***	.08	±.22
Grain	.05**	.02	±.04	.04*	.02	±.05	.04*	.02	±.05
Grain.centred	.08*	.03	±.09	.08*	.03	±.09	.08*	.03	±.09
Extent	−.07*	.03	±.08	−.11***	.03	±.08	−.11***	.03	±.08
Elevation diversity	−.04	.11	±.28	−.02	.11	±.29	−.04	.12	±.30
Habitat mixed				.31**	.11	±.28	.30**	.11	±.28
Habitat non-forest				.08	.12	±.31	.08	.12	±.31
PET				.00	.00	±.00	.00	.00	±.00
Invertebrates							−.08	.12	±.32
Vertebrates							−.03	.08	±.22
(b) Subgroup II									
Intercept	.70***	.20	±.53	.57*	.27	±.72	.54†	.28	±.75
Equal area	−.15	.12	±.32	−.13	.12	±.33	−.11	.12	±.32
Grain	.06*	.03	±.07	.07*	.03	±.08	.05†	.03	±.08
Extent	−.01	.04	±.10	.00	.04	±.12	−.02	.04	±.12
Vegetation complexity	−.24	.15	±.39	−.19	.17	±.45	−.24	.17	±.46
Habitat mixed				−.08	.16	±.43	−.04	.16	±.42
Habitat non-forest				.13	.21	±.56	.17	.22	±.58
Island				.12	.14	±.38	.14	.14	±.37
Vertebrates							.25	.16	±.43

Model 1 tests methodological covariates; models 2 and 3 test location- and taxon-related covariates while accounting for methodology and both methodology and study location respectively. Given are estimates of coefficients *b* for between-study effects (within-study effect for *grain.centred*, i.e. grain centred around the study-level mean), robust standard errors *SE*, and robust 99% confidence intervals *CI* to account for multiple testing. For details on covariates see Table 3.2; reference levels for categorical variables: EH measure category (a) *land cover diversity*, (b) *plant diversity*; habitat *forest*; taxon (a) *plants*, (b) *invertebrates*. R^2 of full model 3: subgroup I: 0.18; subgroup II: 0 (negative R^2, truncated to zero). Significance levels referring to t-test of difference from zero (intercept) or from reference level: ***0.001, **0.01, *0.05, †0.1.

Table 3.4 Results of mixed-effects meta-regression for subgroup III (herbivorous taxa only; covariate: EH subject area; 31/183 studies/data points).

Subgroup III	b	SE	CI
Intercept	1.07***	.16	± .45
Land cover	−.55**	.19	± .53
Topography	−.71**	.22	± .60
Vegetation	−.60	.36	±1.00

Given are estimates of coefficients *b* for between-study effects, robust standard errors *SE* and robust 99% confidence intervals *CI* to account for multiple testing. For details on covariates see Table 3.2; the reference level is *plant diversity*. Model R^2: 0.16. Significance levels referring to t-test of difference from zero (intercept) or from reference level: *** 0.001, ** 0.01.

did not find any significant relationship at all, which was partly attributed to measures inadequate for the given study system, taxon or spatial scale (e.g. August 1983; Monadjem 1999; Marini et al. 2008). Some negative relationships were found between measures of vegetation structure and insect richness, which were ascribed to higher energy cost of movement in denser habitats or to the study taxa being adapted to more open habitats (e.g. Humphrey et al. 1999; Lassau and Hochuli 2004). Furthermore, negative relationships have been found to occur predominantly at small spatial scales (Tamme et al. 2010). Appropriate EH measures are generally taxon dependent, often in interaction with spatial scale: body size and mobility, home range and habitat requirements determine whether a taxon perceives its environment as heterogeneous or is negatively affected by mobility constraints or fragmentation (Tews et al. 2004). Here, we could not test for effects of taxon-specific traits like body size or home range because studies often analysed groups as heterogeneous as mammals and vascular plants. Importantly, even though EH is highly context specific, overall mean effect sizes demonstrate the predominance of positive EH–richness relationships across taxa and EH measures.

3.5.1 EH subject areas and measure categories

Overall, we found positive effects for all five EH subject areas, which makes sense considering that they can all be related to mechanisms promoting species coexistence, persistence and diversification. We found no differences in effects for biotic vs. abiotic EH, but comparing EH subject areas revealed more differentiated patterns: effects for vegetation and topographic EH were larger than for climatic EH. They were also larger than effects for soil EH, although not significantly so (Fig. 3.3). These larger effects make sense because vegetation EH, on one hand, is a more direct driver of species richness, particularly for herbivores, than climatic or soil EH. Vegetation EH is strongly associated with diversity of resources, shelter and roosting, breeding and oviposition sites, and with opportunities for divergent adaptation (e.g. Tews et al. 2004; Novotny et al. 2006; Kissling et al. 2007). By contrast, climatic and soil EH are likely to affect animal species richness indirectly via their effects on vegetation, although direct effects on speciation (Kisel et al. 2011), physiology and ecological preferences of species may also be important. Although the lower effects of climatic and soil EH are plausible given their indirect links to many organisms, we note that their coefficients are least precise due to lower sample size (Fig. 3.3). Topographic EH, on the other hand, acts on richness in more diverse ways than climatic or soil EH: First, regions with high topographic EH have steep climatic and habitat gradients in relatively small areas, thereby promoting spatial turnover of species favouring different conditions (Kerr and Packer 1997; Kallimanis et al. 2008). Second, similar to climate and soil, topographic EH affects animal richness indirectly via its effects on vegetation EH. Finally, topographic EH promotes species persistence and diversification by providing refuges from adverse environmental conditions such as glaciation, and opportunities for diversification through geographic isolation (Rosenzweig 1995; Kallimanis et al. 2010; Särkinen et al. 2012). Therefore, highly heterogeneous tropical mountains may act as cradles and museums of biodiversity and are thus paramount in species richness and concentration of narrow endemics (Hughes and Eastwood 2006; Fjeldså et al. 2012).

In our model including EH measure categories, plant diversity, elevation diversity and land cover diversity showed comparatively large effects (Fig. 3.4). Measures included in these categories are among the most frequently used quantification methods and therefore had higher statistical power to detect an effect. However, it is also likely that these measures are more apt to quantify EH than e.g. patchiness or vegetation dimension. For instance, measures of plant diversity and vegetation complexity likely capture the requirements of many species better than measures of vegetation dimension. Although the taxonomic and functional composition and the physical structure of vegetation are closely linked, results on which component of vegetation EH is more important for herbivore diversity vary (e.g. Haddad et al. 2001; Brose 2003; De Araújo et al. 2013). While higher plant diversity should provide more diverse food resources and opportunities for specialisation, structurally complex vegetation is thought to contain more microhabitats and provide shelter and resting, breeding, oviposition and hibernation sites (Lawton 1983). Even within a single plant species, different herbivores often prefer different structures related to plant organs, vertical stratification, seasonal development or age classes (Lawton 1983). The significance of a particular measure also depends on the degree of specialisation of herbivores (De Araújo et al. 2013).

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

3.5.2 Area constancy

As we expected, area constancy had an important role, as indicated by a significant negative effect of the covariate *equal area* in meta-regressions of subgroup I (EH measure categories elevation and land cover diversity) and by the smaller mean effect size estimate for equal-area studies analysed alone (Table 3.3a, Fig. 3.4). Many EH measures scale positively with area, which makes disentangling the individual effects of EH and area difficult (Ricklefs and Lovette 1999; Triantis et al. 2003). For instance, count or range measures like number of habitat types, number of plant species and elevation range have, on average, larger values for larger areas. When area is not kept constant, effects of EH can therefore be confounded with direct effects of area on species immigration, extinction and speciation rates (compare MacArthur and Wilson 1967; Kisel et al. 2011). Controlling for the effect of area *per se*, the remaining effect of EH is likely to be smaller, as we found. However, we did not find a significant influence of equal area in models of subgroup II (EH measure categories vegetation complexity and plant diversity; Table 3.3b). Although we expected an effect of equal area on plant diversity, measures of vegetation complexity should be less affected by area. This may account for the overall non-significant effect we found, although we did find a negative effect when testing equal area in a single predictor model (−0.31 ±0.36, t =−2.25, P = 0.03), suggesting confounding effects among covariates. Nevertheless, our findings provide strong empirical support for the idea that it is important to keep area constant in studies on EH–richness relationships (compare Whittaker et al. 2001). While methods to model multiplicative effects of EH and area have been proposed (Triantis et al. 2003), statistically controlling for area is problematic as collinearity may obscure the actual effect of EH (Whittaker et al. 2001). We therefore suggest that equal-area study units should be used as much as possible; at least for plot- and grid-based analyses this should be feasible.

3.5.3 Spatial grain and extent

We detected a positive effect of spatial grain in models of subgroups I and II (Table 3.3), also as expected. The fact that we found this effect both between and within studies (Table 3.3a) further stresses the importance of spatial grain, as confounding factors are less likely to be a problem in within- than between-study comparisons. There are multiple possible reasons for positive grain effects: First, larger units on average encompass more variability in EH, making stronger EH–richness relationships more likely (van Rensburg et al. 2002). Second, species turnover and allopatric speciation should become more important at larger spatial scales. Third, negative EH–richness relationships have been found mostly at small spatial scales, where (micro)fragmentation effects that increase the risk of species extinctions through isolation and habitat loss may be stronger (Tamme et al. 2010; Laanisto et al. 2013).

Moreover, small-scale heterogeneity has been suggested to promote the dominance of a few species well adapted to heterogeneous conditions, thereby lowering overall species diversity (Gazol et al. 2013). Interestingly, previous studies have found indications of an opposite trend as well, i.e. of a negative effect of spatial grain on EH–richness relationships (Smith and Lundholm 2012). This may be due to a decline in variation between units occurring when more variation is included within units (Wiens 1989). However, this decline depends strongly on the scale at which environmental variables are measured and vary, and on the distribution and spatial autocorrelation of variable values in an area (Siefert et al. 2012; Smith and Lundholm 2012).

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

We found a negative effect of spatial extent in models of subgroup I (Table 3.3a), which is in line with expectations of EH being more important at intermediate extents and climate being the strongest driver of species diversity at large extents (Sarr et al. 2005; Field et al. 2009). This can partly be explained by the fact that climatic variables usually vary across relatively broad spatial scales (Siefert et al. 2012). Furthermore, some EH might average out with increasing spatial extent (Kolasa and Rollo 1991). The importance of EH is thought to be linked to spatial extent through a hump-shaped relationship (Sarr et al. 2005), but inclusion of a quadratic term in our meta-regressions did not support this idea. Supplementing our database by small-scale studies should give further insights into this topic. We note, however, that many studies did not provide spatial extent and that some of our estimations were inevitably imprecise. We therefore urge authors to provide clear and detailed information on study characteristics (also see Hillebrand and Gurevitch 2013).

3.5.4 Study location

We expected a positive effect of ambient energy, measured as mean PET, as previous studies have found topographic EH to be much more important for mammal and plant species richness in high than in low energy regions (Kerr and Packer 1997; Kreft and Jetz 2007). The surprising lack of a PET effect in our models may partly have been caused by imprecise spatial extents and therefore imprecise PET values in our data set. Also, studies were not evenly distributed spatially across the full range of PET values. A further explanation for our negative findings may be the fact that many study areas were large and thus contained a high variability in PET, which was evened out using mean PET in meta-regressions. To test this, we ran an additional analysis on data points with relatively small spatial extents only, using the first quartile of either the absolute study extent or the latitudinal extent. In both cases, we still did not find a significant effect of PET, which suggests that PET may not be universally related to the strength of EH–richness relationships. However, we suggest that the interaction between energy availability and EH should be considered in future studies. In addition to the effect of physiological constraints, dispersal barriers constituted by topographic EH are likely to be more effective in high-energy regions, where taxa are usually adapted to a smaller range of climatic conditions than taxa in seasonal temperate zones (Janzen 1967). Also, diversification rates are assumed to be higher in high-energy regions (Kisel et al. 2011).

Models of subgroup I suggested a stronger effect of EH in regions with multiple habitat types than in pure forest systems (Table 3.3a). Partly, this may be an artefact because EH measured e.g. as the number of habitat types or elevation range should, on average, be larger for areas covering multiple habitat types. We did not find this effect for subgroup II (Table 3.3b), which indicates that vegetation EH should be less dependent on habitat type. This might be expected because, although plant diversity may also tend to be higher in regions with multiple habitat types, measures of vegetation complexity do not necessarily increase with the addition of habitat types. Although the difference was not statistically significant, effect size estimates for non-forest systems tended to be larger than those for forest systems. This makes sense because key structural elements have been found to be particularly important in non-forest systems such as agricultural fields or grasslands (Tews et al. 2004; Joseph et al. 2011).

3.5.5 Taxonomic and functional groups

We did not detect significant differences among taxa (Table 3.3 and Appendix B.8), suggesting that EH is a universal driver of species richness across taxonomic groups. The surprising similarity in correlates of plant and animal species richness has been pointed out before (Field et al. 2009).

Analysis of subgroup III confirmed our hypothesis that vegetation EH is more important for herbivore richness than climatic or topographic EH (Table 3.4). This is likely due to the close association of plants and herbivores and the expected more direct effects of vegetation EH compared to abiotic EH. However, this relationship is again scale dependent and may get weaker at larger spatial scales (Hawkins and Porter 2003; Field et al. 2009). Also, while our data set did not allow for a more detailed analysis, differentiating between trophic groups or specialist and generalist species in future studies or in focused reanalysis of existing data sets may reveal an even higher importance of plant diversity for specialist species richness (Kissling et al. 2007).

3.5.6 Limitations

Although we aimed to examine a representative subset of the literature, we could only consider simple linear relationships between EH and species richness. The relationship, however, is not necessarily linear: a hump-shaped relationship has been proposed to occur due to an area–heterogeneity trade-off, i.e. a reduction in suitable area available to a particular species associated with increasing EH, which may increase the risk of stochastic extinctions (Kadmon and Allouche 2007). The validity of the area–heterogeneity trade-off hypothesis has been questioned (Hortal et al. 2009, 2013; Carnicer et al. 2013) and was also generally not corroborated by our data set. In fact, hump-shaped or other non-linear EH effects were rarely addressed in the studies that formed our data set, although some relevant studies may have been excluded due to our statistical inclusion criteria. Some studies that did test higher order terms of EH measures found no improvement over linear models or detected saturating or S-shaped, but no decreasing relationships (e.g. Marini et al. 2008, 2011). Only a few studies found quadratic or humpshaped relationships between richness of plants, birds or butterflies and heterogeneity in productivity or land cover types, which were partly attributed to an interaction with productivity levels (Seto et al. 2004; Haberl et al. 2005; Parviainen et al. 2010). The occurrence of quadratic relationships in these studies depended on spatial scale and study taxon, indicating an even higher complexity of EH–richness relationships. The shape of the relationship also depends on the chosen EH measure. For instance, lumbricid species richness was found to be linked to the percentage of forest cover by a hump-shaped relationship, whereas it was positively linked to the number of habitat types, which probably increased with decreasing forest cover (Vanbergen et al. 2007). Overall, authors who found hump-shaped or negative EH–richness relationships often related their findings to an inadequate quantification of relevant EH components and not to a potential area–heterogeneity trade-off. More frequent investigations of non-linear relationships in future studies or reanalyses of existing data sets should help resolving the question of the existence of and reasons behind hump-shaped EH–richness relationships.

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

3.5.7 Publication bias

We detected some taxonomic and geographical bias in the EH–species richness literature, but the broad scope of our analysis and our use of random-effects models allows for reasonable generalisations. Furthermore, we consider our conclusions robust to publication bias: First, in cases where we detected funnel plot asymmetry, no indication of asymmetry remained when we considered equal-area studies only or residuals of mixed-effects models. This implies that asymmetry was caused by heterogeneity in the data rather than by publication bias, and that the heterogeneity was partly accounted for by the covariates (Nakagawa and Santos 2012). Second, although based on a fixed-effects model of study-level means and therefore not directly comparable to the models in our analysis, the large failsafe number of 211 470 implies robustness of our results. Third, publication bias is expected to be less problematic in biological studies, which often report tests of multiple hypotheses and therefore often contain both significant and non-significant results (Jennions et al. 2013). This lines up with the relatively high number of non-significant data points in our analysis as well as the fact that most studies investigated multiple environmental variables. Moreover, we calculated some effect size estimates ourselves that were thus not subject to publication bias.

3.6 Conclusions

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

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

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4

Differential effects of environmental heterogeneity on global mammal species richness

4.1 Abstract

Spatial environmental heterogeneity (EH) is an important driver of species richness, affecting species coexistence, persistence, and diversification. According to its central role in ecological research, EH has been widely studied and quantified in many different ways. However, a strong bias regarding the calculation and use of EH measures can be found in the literature, which is dominated by a few common EH measures like elevation range. Here, we systematically calculate and compare 51 EH measures across three spatial grains and at global extent. These measures are based on nine different variables related to the subject areas land cover, vegetation, climate, soil, and topography, and on nine different calculation methods. We explore the collinearity among EH measures and identify regions that are similar or different with regard to particular EH measures or multidimensional EH space based on principal component analysis. Despite some redundancy, partly weak correlations ($\rho = -0.45$ to 1.00, median 0.35) and differential spatial patterns indicate clear differences between measures, which thus represent different aspects of EH. Moreover, we analyse the relationship between each EH measure and species richness of global terrestrial mammals and identify measures that are most closely associated with mammal richness after accounting for the effects of current climate, regional biogeographic history and human influence. We find a clearly differential importance of EH subject areas and calculation methods for global mammal species richness. Measures of climatic and topographic EH and measures calculated as counts and ranges emerge as particularly strongly related to mammal richness across all spatial grains. Our results highlight that methodological decisions, including measure calculation and statistical analysis, greatly determine the outcome of EH–richness studies. These decisions should therefore be made carefully with regard to the hypothesis and mechanism of interest.

4.2 Introduction

Spatial environmental heterogeneity (EH) is an important determinant of species richness gradients worldwide (Rosenzweig 1995; Tews et al. 2004; Stein et al. 2014). EH is generally thought to enhance species richness through three mechanisms (compare Stein and Kreft 2014): First, an increase in resources, structural complexity, and environmental conditions should increase the available niche space and thereby promote species coexistence (Hutchinson 1959; Currie 1991; Tews et al. 2004). Second, EH should enhance species persistence through the provision of shelter and refuges from adverse environmental conditions such as glaciations (Svenning and Skov 2007; Cousin and Phillips 2008). Finally, EH should increase the probability of species diversification through isolation or adaptation to diverse environmental conditions (Pianka 1966; Hughes and Eastwood 2006; Kallimanis et al. 2010). Different aspects of EH thereby affect ecological and evolutionary processes.

EH has been quantified by a wide range of measures related to five different subject areas, i.e. land cover and vegetation as biotic components of EH, and climate, soil, and topography as abiotic components (compare Stein and Kreft 2014). EH measures have most often been calculated as ranges (e.g. range in elevation or precipitation), counts (e.g. number of land cover types or plant species) or indices (e.g. Simpson index of land cover types; foliage height diversity), but other calculation methods, such as percentages or standard deviations (e.g. percentage of forest cover; standard deviation of soil pH), have also been used. Overall, more than 160 different measures with many variations exist in the literature (Stein and Kreft 2014). Due to the different calculation methods and underlying variables, these measures represent various aspects of EH (compare Bouchet et al. 2014). For instance, range measures capture the length of environmental gradients, while indices may contain information about the variability or configuration of environmental variables within study units. Index measures like foliage height diversity or plant species diversity, for instance, have been used to quantify the structural and taxonomic complexity of vegetation as a proxy for resource diversity and the availability of resting, hiding, and breeding sites (e.g. MacArthur and MacArthur 1961; Gonçalves-Alvim and Fernandes 2001). Other measures, such as the number of land cover or soil types and the range in temperature or precipitation, relate more to the spatial turnover of species with different environmental requirements (e.g. Johnson and Simberloff 1974; Ricklefs and Lovette 1999). Elevation range is a relatively broad proxy of habitat turnover, isolation and diversification probabilities, and refugial opportunities (Rahbek and Graves 2001; Kallimanis et al. 2010). Other measures of topographic EH that consider slope, aspect or ruggedness, relate more to microclimatic and edaphic conditions such as insolation, water drainage, and wind exposure, and may thereby also refer to the availability of resting, nesting, and foraging sites (Bouchet et al. 2014). The relevance of EH measures thus also depends on spatial scale, and measures of vegetation structure, for instance, should be more important at smaller spatial scales, where niche differentiation and biotic interactions play a larger role. At larger scales, climatic or topographic EH measures related to spatial turnover or isolation should become more relevant.

Depending on the study taxon and its relationship with the abiotic and biotic environment, different EH subject areas should be important. For terrestrial animals and plants in general, the relationship between EH and species richness has been found to be strongest for topographic and vegetation EH (Stein et al. 2014), but the strength of EH–richness relationships depends on spatial scale and taxon-specific characteristics like body size, range size, mobility or trophic group (Huston 1994; Rahbek and Graves 2001; Tews et al. 2004; Stein et al. 2014). Consequently, studies comparing multiple EH measures have found variable associations between EH and species richness (e.g. Kerr and Packer 1997; Priego-Santander et al. 2004; Parviainen et al. 2010). Most studies include EH measures related to only one or few subject areas, and the literature is generally biased with regard to the variability in subject areas and EH measures. For instance, while land cover EH has been quantified by many different measures and calculation methods, topographic EH has been quantified by elevation range in most studies (Stein and Kreft 2014). A recent meta-analysis revealed an underrepresentation of climatic and soil EH in studies conducted at landscape to global extents (Stein et al. 2014). The literature on EH–richness relationships is overall dominated by a few common measures including the number of plant species, the number or Shannon entropy of land cover types, and, most commonly, elevation range (Stein and Kreft 2014). Also in broad-scale vertebrate studies, EH has mostly been quantified by common measures such as the number or diversity of land cover types and elevation range (e.g. Jetz et al. 2009; Qian 2010; Fløjgaard et al. 2011). While elevation range is often easily available, it may miss important aspects of EH including topographic slope and ruggedness, which other calculation methods such as derived indices may cover.

Here, we systematically calculate and compare a series of EH measures across three spatial grains and at global extent using different variables and calculation methods that are relatively easily available. We cover different dimensions of biotic and abiotic EH by including variables representing all five subject areas (following Stein and Kreft 2014), i.e. land cover, vegetation, climate, soil, and topography. We investigate how variable or redundant these EH measures are using correlation and ordination techniques. Furthermore, we test to what extent the different EH measures vary in their ability to explain terrestrial mammal species richness worldwide. We are particularly interested in whether study outcomes are affected more by the choice of subject area or by the calculation method of EH measures.

4.3 Methods

4.3.1 Environmental data

Variables used for EH measures We derived EH measures for the five subject areas from nine different environmental variables. (1) Land cover EH was represented by (a) land cover classes according to the global land cover product GLC2000 (GLC; Global Land Cover 2000 database 2003), including 22 different classes; (b) annual net primary production (NPP; 0.1 gC/m^2) from the MOD17 MODIS project as a thirteen-year average (2000–2012; Zhao and Running 2010). Land cover EH based on these variables should thus represent the spatial turnover of environmental conditions, habitat types and energy availability, which are thought to be important for mammal species richness (e.g. Fraser 1998; Moreno-Rueda and Pizarro 2007; Qian and Kissling 2010). (2) Vegetation EH was quantified based on (a) vascular plant species richness (PLA) using predictions based on kriging interpolation from Kreft and Jetz (2007); (b) canopy height (m; VEG) from the 3D Global Vegetation Map based on radar and lidar remote sensing (Simard et al. 2011). While plant species richness is used as a proxy of resource diversity, EH measures derived from canopy height should represent structural complexity of the vegetation and therefore relate to important habitat characteristics such as resting, hiding, overwintering, and foraging sites (Kitchener 1982; Lawton 1983; Horváth et al. 2001). (3) Climatic EH was represented by energy and water variables that are well-known determinants of species richness of mammals and other taxa (e.g. Currie 1991; Kerr and Packer 1997): (a) annual mean temperature (TEM; converted to Kelvin) from the WorldClim dataset (Hijmans et al. 2005); (b) annual precipitation (PRE; mm; Hijmans et al. 2005); (c) mean annual potential evapotranspiration (PET; mm; averaged over 1950–2000; Trabucco and Zomer 2009). (4) Soil EH was determined through major soil groups (SOI) from the Harmonized World Soil Database (FAO/IIASA/ISRIC/ISSCAS/JRC 2012), including 35 different classes. Measures of soil EH have been found to affect mammal species richness before (e.g. Rosenzweig and Winakur 1969; Fraser 1998) and should cover direct effects on burrowing and soil dwelling mammals as well as indirect effects through vegetation turnover. (5) Topographic EH was based on elevation (ELE; m a.s.l.; values shifted to ≥ 0 by adding the absolute minimum, 431 m; Hijmans et al. 2005). Various EH measures derived from elevation are likely to correlate with mammal species richness due to the close association between topographic EH and climatic gradients, habitat turnover, and isolation probabilities (compare, e.g. Kerr and Packer 1997; Fraser 1998; Joly and Myers 2001; Bouchet et al. 2014).

All variables except for vascular plant species richness had a resolution of 30 arcsec or approximately 1 km at the equator. Vascular plant species richness was available at a resolution of 12,364 km^2, which was the smallest grain size used in our analyses.

EH measure calculation We calculated EH measures for global equal-area grid cells of 12,364 km^2 (approximately 111 km × 111 km at the equator). To test for the influence of spatial grain on EH–

richness relationships, we also calculated all measures separately for two larger grain sizes, i.e. grid cells of 49,457 km² (approximately 222 km × 222 km at the equator) and 197,829 km² (approximately 444 km × 444 km). Vascular plant species richness, which we consider an EH measure as it is, was the only exception. As area and species richness are not linearly related (Arrhenius 1921) and to avoid additional assumptions, we calculated PLA for the two larger grain sizes as mean plant species richness per grid cell based on the values of the smallest grain. The main focus of our study lies on this smallest grain size; our results therefore refer to the 111 km × 111 km grain, if not stated otherwise.

We applied nine different calculation methods in total. For each of the two categorical variables GLC and SOI, we calculated three EH measures (compare Magurran 2004), i.e. count (number of classes; *co*), Simpson index (*si*; 1−D, where $D = \Sigma p_i^2$, and p_i = proportion of the *i*th class), and Shannon entropy (*sh*; $H = -\Sigma p_i \ln p_i$). With the number and diversity of environmental classes we aimed to relate to spatial turnover of species with different habitat requirements. We also calculated these measures for the continuous variables (NPP, VEG, TEM, PRE, PET, ELE) after classifying each variable into 50 equal-interval classes. To avoid spatial bias in the derived EH measures due to artificial class breaks, we also shifted the breaks up and down seven times each in small steps until the centre of the adjacent upper or lower class (resulting in the original breaks, seven up-shifted breaks and seven down-shifted breaks). Each time, we computed the respective EH measure and used the mean of these fifteen outcomes in our analysis. Furthermore, we calculated the following measures for continuous variables: range (*ra*; maximum−minimum), standard deviation (*sd*), coefficient of variation (*cv*; set to zero in case of zero mean), and terrain ruggedness index (*tri*; mean per grid cell of the mean of absolute differences between the values of a pixel and the values of its eight neighbouring pixels; Riley et al. 1999; Wilson et al. 2007). While *ra* measures cover the length of environmental gradients, *sd*, *cv*, and *tri* measures capture variability among sampling units. As this variability is difficult to interpret disregarding the mean value of a variable, *cv* accounts for this by dividing the standard deviation by the mean. *Tri* is a more detailed proxy of terrain heterogeneity and designed to approximate structural attributes like cover for prey or predators (Riley et al. 1999), which of course depends on the underlying data resolution. For VEG, we additionally calculated mean (*me*) and maximum (*ma*) canopy height as further proxies of vegetation structural complexity. This resulted in 51 EH measures overall. All variables were extracted and EH measures calculated in R (R Core Team 2013), using the packages *maptools*, *raster*, *rgdal*, *rgeos*, and *vegan* (Bivand and Lewin-Koh 2013; Hijmans 2014; Bivand et al. 2013; Bivand and Rundel 2014; Oksanen et al. 2013).

Further covariables It is well documented that species richness of terrestrial vertebrates is strongly influenced by current climate, more specifically by water and energy availability (e.g. Hawkins et al. 2003b; Qian 2010). We therefore chose three variables that have been deemed important for broad-scale mammal richness (Kerr and Packer 1997; Qian 2010; Davies et al. 2011; Hawkins et al. 2012) to account for in all our models, namely annual actual evapotranspiration (AET; mm, Ahn and Tateishi 1994), TEM and PRE. For each variable, we calculated the mean value per grid cell. AET was only available at a resolution of 30 arcmin and was disaggregated to 1 km for the calculation of the mean. As AET and PRE were highly correlated in our dataset ($r = 0.91$), we only included AET in our models, which incorporates water-energy dynamics and is a coarse proxy for productivity, and which emerged as the most important predictor of mammal richness in several studies (Ruggiero and Kitzberger 2004; Qian 2010; Davies et al. 2011). To account for regional and historical effects, which have been shown to be important for global mammal richness before (e.g. Hortal et al. 2008), we also included seven biogeographic mammal regions (REG) derived from UPGMA clustering of the same distribution data (Kreft and Jetz 2010) in all models. Moreover, we included the Global Human Influence Index (HII) to account for anthropogenic impacts (Sanderson et al. 2002; Wildlife Conservation Society - WCS, and Center for International Earth Science Information Network - CIESIN - Columbia University 2005).

4.3.2 Mammal data

Our analysis included distribution ranges of 5,282 terrestrial mammal species worldwide from the IUCN Redlist of Threatened Species (IUCN 2013). We used historical ranges, including (probably) extant and (possibly) extinct species and species with uncertain presence. We excluded introduced and vagrant species and species of uncertain origin. We calculated species richness separately for the three grain sizes. A species was considered present in a grid cell if any part of its range lay within cell boundaries. Species richness was computed as the number of species present in each grid cell.

4.3.3 Statistical analysis

Many EH measures are correlated with area, which hampers disentangling the separate effects of EH and area *per se* (Triantis et al. 2003; Stein et al. 2014). We therefore aimed at keeping the area of study units constant in each analysis. To this end, we excluded all coastal cells of mainlands and islands, leaving 9,131 grid cells with terrestrial mammals at the smallest grain size. Exclusion of large inland water bodies based on the GADM database (Global Administrative Areas 2012) and of grid cells for which not all environmental variables were available left 8,914 grid cells for the analysis. The analyses conducted at the two larger spatial grains were based on 2,003 and 399 grid cells, respectively.

We first explored the similarity among EH measures by Spearman rank correlation and principal component analysis (PCA). We also visualised the similarity in EH among geographic regions by colouring a global map according to the position of each grid cell in the PCA. To this end, red, green, and blue components of RGB colour space were assigned to each PCA point according to its position along the first three PCA axes.

As many measures were correlated, we analysed their effects on mammal species richness in separate models. We first ran simple ordinary least squares (OLS) regressions between each EH measure and mammal species richness. We also ran multi-predictor OLS models including one EH measure at a time in addition to the control variables AET, TEM, HII and REG. We compared these models to a model including only AET, TEM, HII and REG without any EH measure. The high amount of variance explained by these covariables alone and the fact that climatic and, to a lesser extent, regional effects have been deemed most important for global mammal species richness (Hawkins et al. 2003a; Hortal et al. 2008), indicated that the multi-predictor models give a more meaningful picture than single-predictor models. Therefore, we focused on multi-predictor models in the remaining analyses. To examine the effect of spatial grain, all models were computed separately for the three grain sizes. Mammal species richness was square-root transformed and some EH measures were log transformed, based on data exploration including scatterplots with LOESS smoothers (Quinn and Keough 2002; Zuur et al. 2010; see Table 4.1). If variables contained zero, we added one half of the smallest non-zero value before log transformation. Models were then computed with all variables standardised to z scores (Quinn and Keough 2002).

We detected considerable spatial autocorrelation in OLS model residuals by inspection of Moran's I-based correlograms (Dormann 2007; Appendix Figs. C.1 to C.3). As spatial autocorrelation violates the assumptions of independence and identical distribution of model residuals, it inflates type I errors and may lead to poor parameter estimates and biased model comparison (Legendre 1993; Cassemiro et al. 2007; Dormann 2007). We therefore accounted for spatial autocorrelation by simultaneous autoregressive (SAR) models of the error type, defining the neighbourhood structure based on the Akaike Information Criterion (AIC) and minimum residual spatial autocorrelation (Kissling and Carl 2007). Spatial weights matrices for the three grain sizes were based on row standardisation and neighbourhood distances of 150 km, 300 km, and 550 km, respectively. Hereby, residual spatial autocorrelation was reduced to negligible levels (Figs. C.1 to C.3). Although we present OLS model results for comparison, the main part of our analysis is based on SAR models. We calculated pseudo R^2 values as the squared

Pearson correlation coefficient between observed and predicted values separately for the non-spatial and the spatial term (Kissling and Carl 2007; Hanspach et al. 2011). SAR models were implemented in R (R Core Team 2013) with the package *spdep* (Bivand 2014).

We compared the association of EH measures with global mammal species richness based on model AIC. As many EH measures were correlated, we did not focus on the exact order of measures in the AIC ranking. Instead, we determined whether the subject area or calculation method of EH measures was more important for SAR model support using conditional inference trees (Hothorn et al. 2006). In this binary recursive partitioning framework, splits in a tree are based on the strength of association between the response variable, i.e. ΔAIC of SAR models, and the input variables, i.e. subject area and calculation method. In each step, the null hypothesis of independence between each single input variable and the response variable is tested. The input variable with the strongest association with the response variable is selected according to the corresponding p-value, and the data are split into two groups based on this input variable. We implemented conditional inference trees with the R package *party* (Hothorn et al. 2006), using MonteCarlo testing and a stop criterion of 0.5. The splitting thus continued as long as $1 - p$-value exceeded this stop criterion.

4.4 Results

4.4.1 EH measures

We detected weak to strong collinearity among EH measures and even negative correlations, depending on the underlying variables and calculation methods used (Fig. 4.1; Tables C.1 to C.3). Spearman rank correlations ranged from −0.45 to 1.00, with relatively low median and mean correlations of 0.35 and 0.43, respectively. Consequently, global maps of EH measures revealed similar patterns in some cases (compare, e.g., different calculation methods for ELE, PET and TEM in Figs. C.4 to C.6), but also clear differences (Fig. 4.2). Some EH measures, e.g. those based on SOI and GLC, were relatively distinct from other measures (Fig. 4.1; Tables C.1 to C.3; Figs. C.4 to C.6). While the Andes and Himalayas regions were characterised by high climatic and topographic EH (Figs. 4.2a and C.4), large parts of Eurasia, among other regions, showed particularly high soil and land cover EH based on GLC (Figs. 4.2b and C.4). Different measures of vegetation EH were particularly high in tropical South America, south-east Asia and central Africa (Figs. 4.2c and C.4).

Principal component analysis of all 51 EH measures revealed that 70.7% of the variation was accounted for by the first three principal components (Fig. 4.3; also see Fig. C.7). The first component, accounting for 45.1% of the variation, was mainly correlated with measures of climatic and topographic EH (Fig. 4.3a and b; Table C.4). The second component (18.4%) mainly represented measures of land cover and vegetation EH, in particular NPP, PLA, and VEG measures (Fig. 4.3a and c; Table C.4). Correlations were mostly positive except for *cv* and *tr* measures. The third component (7.1%) was most strongly positively correlated with PRE measures and was most strongly and negatively correlated with GLC and SOI measures (Fig. 4.3b and c; Table C.4). While the first component was positively correlated with mean elevation ($r = 0.51$), the second component was negatively correlated with mean elevation ($r = -0.46$) and notably positively correlated with mean AET ($r = 0.67$). Consequently, the visualisation of PCA space on a global map, which illustrates the similarity in EH among regions, mainly highlighted areas of high topographic EH and some particularly arid areas (Fig. 4.3 d).

4.4.2 EH–richness relationship

Mammal species richness ranged from seven to 252 species per grid cell at the 111 km × 111 km grain (10 to 277 and 12 to 336 species, respectively, at the 222 km × 222 km and 444 km × 444 km grains)

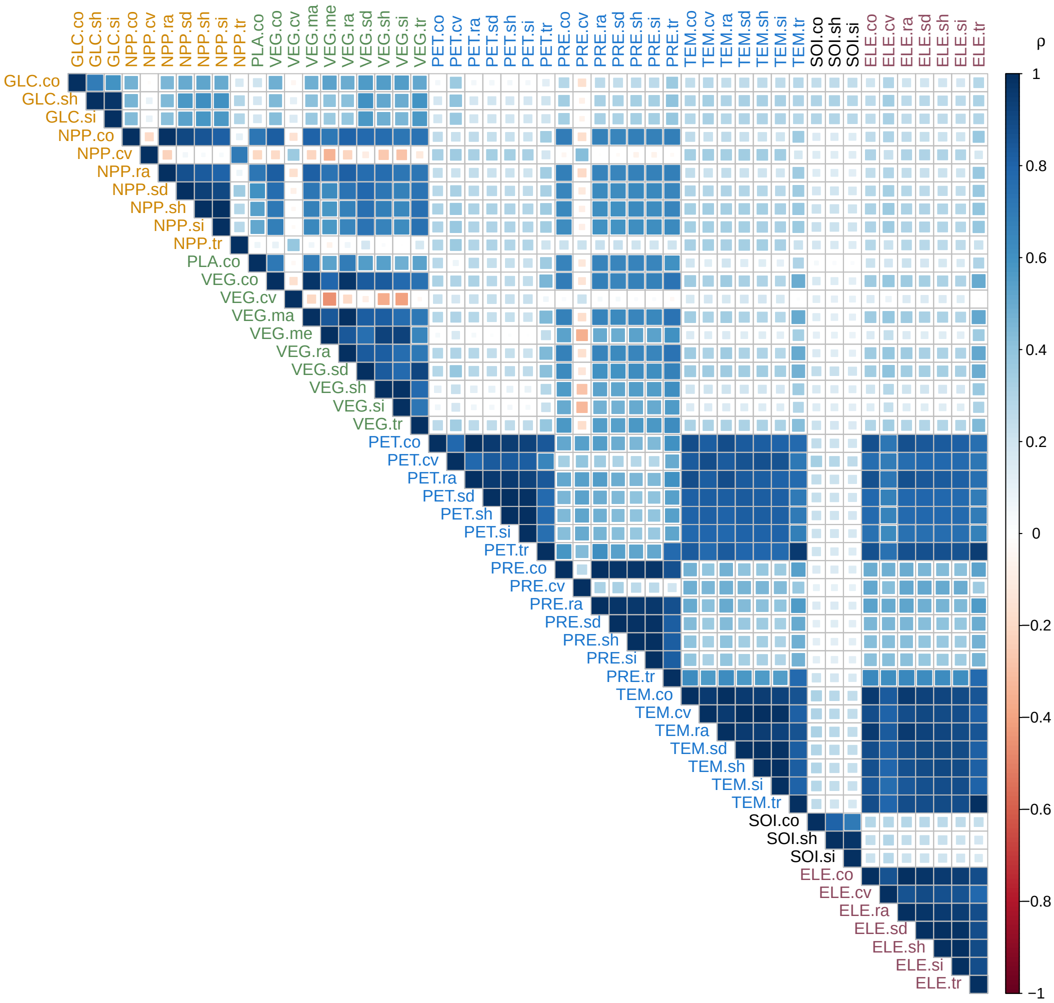

Figure 4.1 Spearman rank correlations ρ among 51 global environmental heterogeneity (EH) measures. Colour squares signify correlations according to the legend; square size is proportional to absolute correlation values. Abbreviated measure names consist of three letters for each variable and two letters for calculation methods, e.g. ELE.sd, standard deviation of elevation. Variables: ELE, elevation; GLC, land cover classes; NPP, annual net primary production; PET, mean annual potential evapotranspiration; PLA, vascular plant species richness; PRE, annual precipitation; SOI, major soil groups; TEM, annual mean temperature; VEG, canopy height. Calculation methods: co, count; cv, coefficient of variation; ma, maximum; me, mean; ra, range; sd, standard deviation; sh, Shannon entropy; si, Simpson index; tr, terrain ruggedness index. Colours of EH measures names are according to the five subject areas land cover (yellow), vegetation (green), climate (blue), soil (black), and topography (violet).

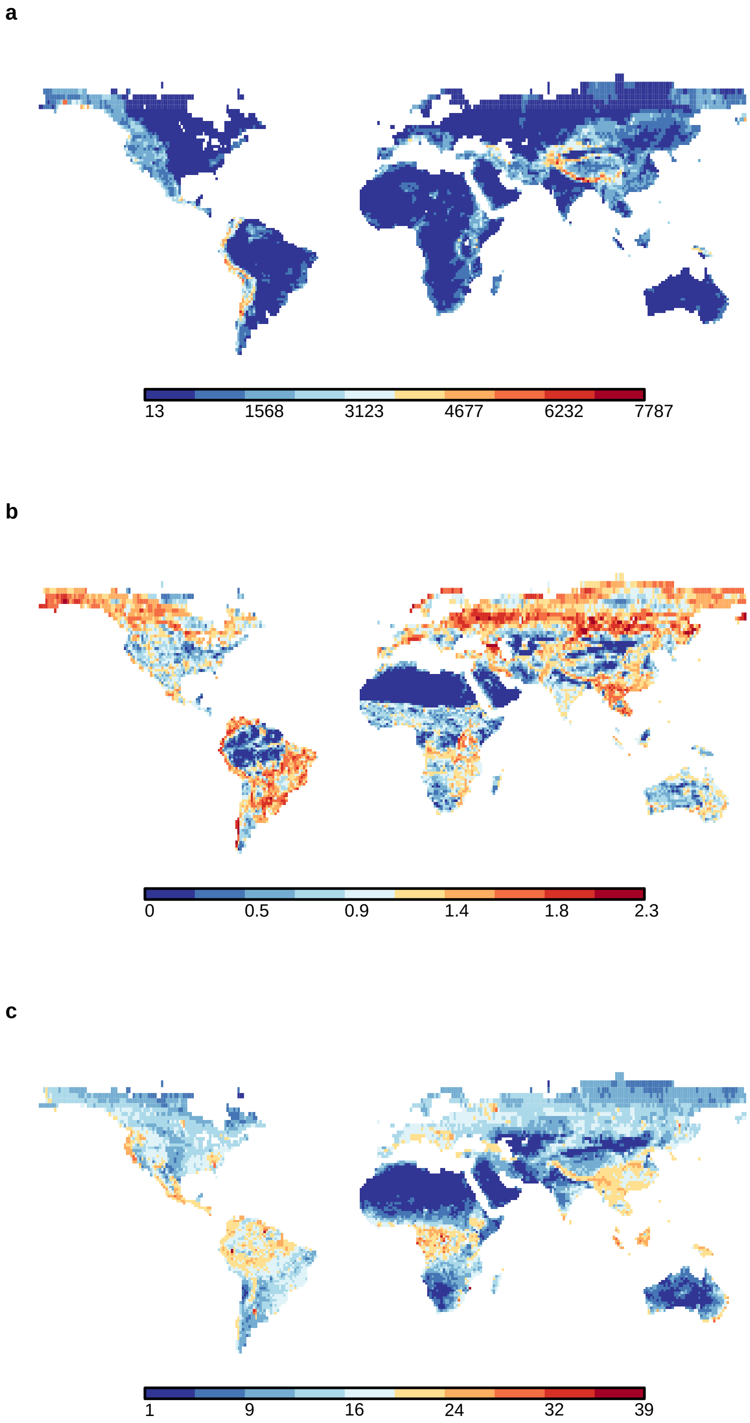

Figure 4.2 Exemplary maps of EH measures at 111 km × 111 km grain; for a complete set of maps see Figs. C.4 to C.6. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. (a) Elevation range (ELE.ra; m a.s.l.; raw elevation values were shifted to ≥ 0 by adding the absolute minimum, 431 m); (b) Shannon entropy of global land cover classes (GLC.sh); (c) number of vegetation height classes (VEG.co). Colours represent ten equal classes per EH measure according to the legend.

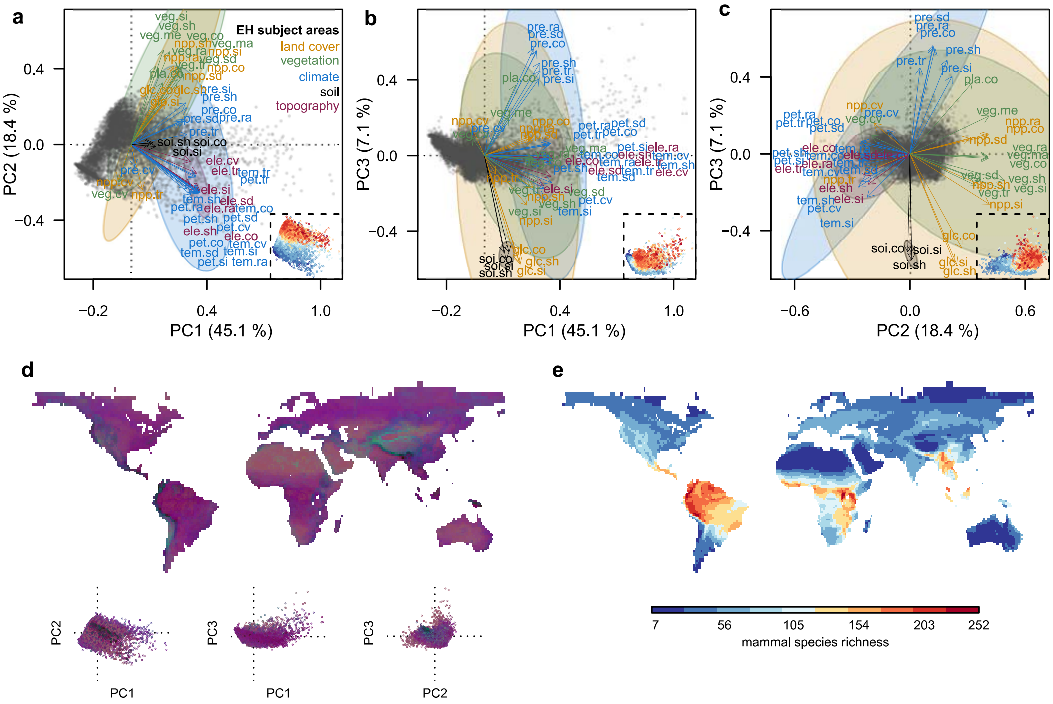

Figure 4.3 Principal components analysis (PCA) of EH measures. (a-c) First three axes of PCA including all 51 EH measures. Numbers in parentheses indicate the percentage of variance accounted for by each axis. Colours of arrows, EH measure names and illustrative ellipses correspond to EH subject area. Points represent grid cells and are coloured according to mammal species richness in the insets (compare panel (e)). Text labels are slightly shifted for clarity. For abbreviations, see Fig. 4.1. (d) PCA as in (a-c), where the PCA points are coloured based on their position in a three-dimensional colour space (small plots). Similar colours on the map illustrate similarities in EH space among regions. (e) Mammal species richness per grid cell.

and increased pronouncedly towards the equator. Highest species richness occurred in the Andean and Afromontane regions, followed by south-east Asia (Fig. 4.3e; compare Schipper et al. 2008). Regions with high mammal species richness coincided mainly with land cover and vegetation EH and PRE measures in PCA plots (Fig. 4.3e and insets in a–c).

Comparing the association of EH measures with global mammal species richness, we detected clear differences between single- and multi-predictor SAR models. In single-predictor models and at fine spatial grain, plant species richness (PLA) received by far the highest model support according to AIC, solely explaining 61% of the variation in mammal species richness (Table 4.1). Next in AIC rank were count (*co*) and range (*ra*) measures of TEM and ELE, although the respective models explained only 3% of the variation. While the number of precipitation classes gained highest support at the two coarser grains, the amount of variance explained and standardised regression coefficients for PLA remained considerably high across spatial grains (Tables 4.1 to 4.3). Supporting our observations from the PCA plots, also other measures of vegetation EH and NPP received relatively high model support in single-predictor models, which decreased in multi-predictor models (Tables 4.1 to 4.3). In multi-predictor models, also the support for PLA clearly decreased, whereas measures of climatic and topographic EH gained strongest support across all three grain sizes. In particular, mostly *co* and *ra* measures of TEM, PET, and ELE were favoured according to AIC, with minor differences in ranks among grains. Also different measures of PRE were relatively strongly supported (Tables 4.1 to 4.3; Fig. 4.4).

The multi-predictor SAR model that only accounted for mean AET, TEM, biogeographic regions (REG) and human influence (HII) without including EH explained 63% to 69% of the variation in mammal species richness, depending on spatial grain (Tables 4.1 to 4.3). The amount of variation explained by EH measures alone in addition to the shared variance in multi-predictor models ranged from 8% to 12% and was largest at the coarsest grain.

The described differences in model support among EH measures were confirmed by conditional inference trees, which revealed a significant split between EH subject areas in the first step (Fig. 4.5). At the two finer grain sizes, climatic and topographic EH were associated with lower ΔAIC values, i.e. higher model support, than land cover, vegetation, and soil EH (Fig. 4.5a and b). At the coarsest grain, land cover EH shared the first tree branch associated with lower ΔAIC values with climatic and topographic EH (Fig. 4.5c). The second partitioning step separated calculation methods at all grain sizes, but only for climatic, land cover, and topographic EH in case of the coarsest grain (Fig. 4.5). *Co*, *ra* and standard deviation (*sd*) measures were among the best EH measures with respect to AIC, however, this depended on the associated variables and subject areas (Figs. 4.4 and 4.5). EH measures based on coefficient of variation (*cv*), Simpson index (*si*) and terrain ruggedness index (*tr*) performed comparatively poorly overall, although tree splits had low significance in case of climatic and topographic EH at the finest grain (Fig. 4.5a).

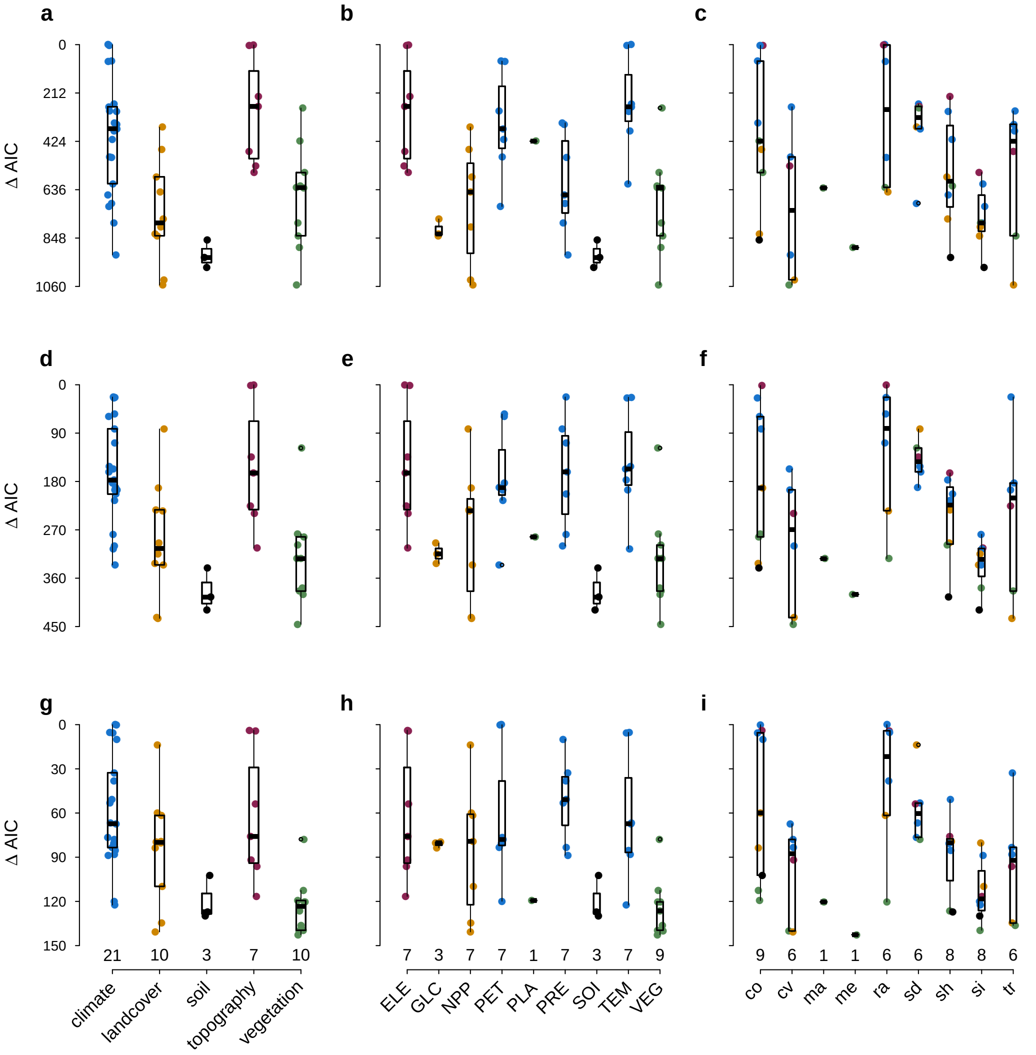

Figure 4.4 Box-whisker plots showing ΔAIC-based model support of multi-predictor SAR models including one EH measure at a time while accounting for mean actual evapotranspiration, annual temperature, biogeographic regions and human influence index. Models are based on three spatial grains: (a-c) 111 km × 111 km grid; (d-f) 222 km × 222 km grid; (g-i) 444 km × 444 km grid. Boxes and horizontal lines represent the first and third quartiles and the median per group. Whiskers extend to extreme data points that are within 1.5 times the interquartile range from the box; circles represent outliers beyond this range. Groups are based on (a, d, g) EH subject area, (b, e, h) variable, and (c, f, i) calculation method. Numbers along x-axes give the numbers of EH measures per group. Jittered dots represent the ΔAIC values associated with each model and are coloured by subject area as in (g). For abbreviations, see Fig. 4.1.

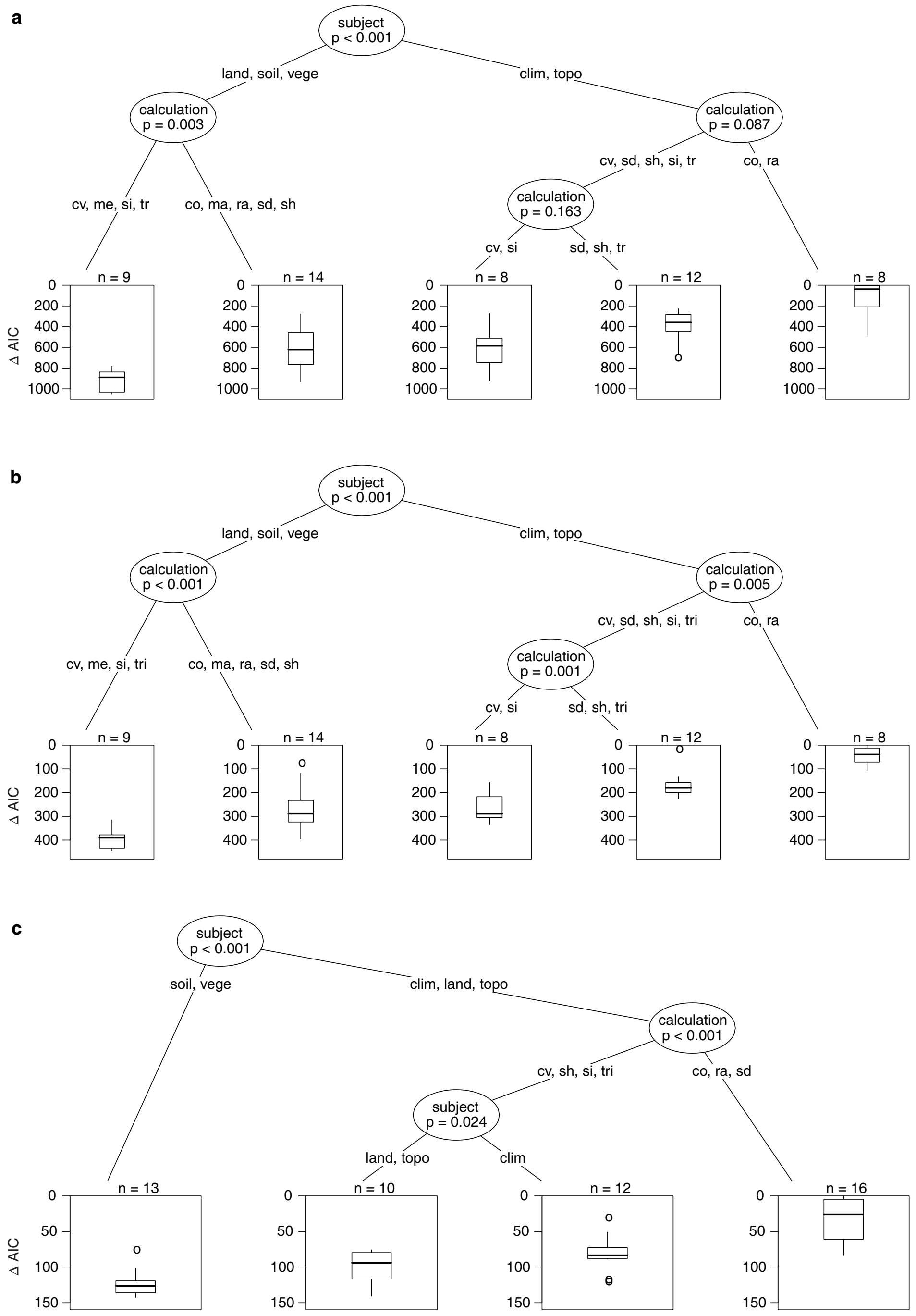

Figure 4.5 Conditional inference trees illustrating whether subject area or calculation method of EH measures is a stronger determinant of ΔAIC-based model support in multi-predictor SAR models. Splits in conditional inference trees are based on the strength of association between the response variable, ΔAIC, and the input variables, i.e. subject area and calculation method. In each step, the data are split into two groups based on the input variable with the strongest association with ΔAIC according to a *p*-value. Conditional inference trees are based on models from three spatial grains: (a) 111 km × 111 km, (b) 222 km × 222 km, (c) 444 km × 444 km grid. Box-whisker plots represent the interquartile range around the median ΔAIC (boxes). Whiskers extend to extreme data points that are within 1.5 times the interquartile range from the box; circles represent outliers beyond this range. Abbreviations: subject, EH subject area; calculation, calculation method; clim, climatic EH; land, land cover EH; soil, soil EH; topo, topographic EH; vege, vegetation EH. For abbreviations of calculation methods, see Fig. 4.1.

Table 4.1 Single- and multi-predictor simultaneous autoregressive (SAR) and ordinary least-squares (OLS) models including environmental heterogeneity (EH) against mammal species richness (111 km × 111 km grain). Multi-predictor models include mean AET, TEM, REG, HII, and one EH measure each (or no EH measure, i.e. *covariables only*). Mammal species richness was square-root transformed, EH measures were log transformed where indicated. Given are ΔAIC, R^2 (pseudo R^2 for the non-spatial term in SAR models, adjusted R^2 for OLS models) and standardised regression coefficient *b* for each model type. Significance levels: *** 0.001, ** 0.01, * 0.05. The ten lowest ΔAIC values per model type are shown in bold. For abbreviations, see Fig. 4.1.

		SAR						OLS					
		single-predictor model			multi-predictor model			single-predictor model			multi-predictor model		
	EH measure	ΔAIC	R^2	b	ΔAIC	R^2	b	ΔAIC	R^2	b	ΔAIC	R^2	b
land cover	GLC.co	861.61	.03	$.05^{***}$	830.20	.64	$.05^{***}$	8217.83	.03	$.17^{***}$	1833.95	.78	$.15^{***}$
	GLC.sh	795.90	.04	$.05^{***}$	764.35	.65	$.04^{***}$	8099.18	.04	$.20^{***}$	1457.49	.79	$.17^{***}$
	GLC.si	864.32	.04	$.04^{***}$	837.99	.65	$.04^{***}$	8074.18	.04	$.21^{***}$	1361.65	.80	$.17^{***}$
	NPP.co	257.67	.45	$.12^{***}$	460.29	.67	$.10^{***}$	**3068.50**	.45	$.67^{***}$	1390.48	.79	$.22^{***}$
	NPP.cv^{log}	1068.04	.05	$.01^{***}$	1030.89	.63	$.01^{***}$	8049.55	.05	$-.22^{***}$	2143.93	.78	$.03^{***}$
	NPP.ra	468.12	.46	$.10^{***}$	646.48	.67	$.08^{***}$	**3016.03**	.46	$.68^{***}$	1489.70	.79	$.21^{***}$
	NPP.sd	309.48	.28	$.07^{***}$	361.84	.65	$.06^{***}$	5534.97	.28	$.53^{***}$	1586.72	.79	$.15^{***}$
	NPP.sh	412.81	.30	$.10^{***}$	579.47	.67	$.09^{***}$	5267.87	.30	$.55^{***}$	967.72	.80	$.26^{***}$
	NPP.si	697.01	.28	$.09^{***}$	798.47	.68	$.07^{***}$	5504.97	.28	$.53^{***}$	854.89	.81	$.29^{***}$
	NPP.tr	1076.96	.02	$.00^{*}$	1054.46	.63	.00	8324.35	.02	$-.13^{***}$	2136.99	.78	$.03^{***}$
vegetation	PLA.co	**0.00**	.61	$.55^{***}$	423.22	.72	$.46^{***}$	**0.00**	.61	$.78^{***}$	1104.13	.80	$.30^{***}$
	VEG.co	403.12	.45	$.09^{***}$	560.94	.67	$.07^{***}$	**3105.15**	.45	$.67^{***}$	1210.57	.80	$.27^{***}$
	VEG.cv^{log}	1081.83	.00	.00	1053.61	.63	.00	8472.92	.00	.00	1787.29	.79	$.10^{***}$
	VEG.ma	502.52	.45	$.09^{***}$	628.03	.67	$.07^{***}$	**3108.95**	.45	$.67^{***}$	1358.57	.80	$.27^{***}$
	VEG.me	754.89	.35	$.08^{***}$	889.67	.64	$.06^{***}$	4619.04	.35	$.59^{***}$	2165.89	.78	$.03^{***}$
	VEG.ra	506.50	.45	$.08^{***}$	625.61	.67	$.07^{***}$	**3171.28**	.45	$.67^{***}$	1340.38	.80	$.27^{***}$
	VEG.sd	**110.06**	.27	$.09^{***}$	277.72	.66	$.08^{***}$	5641.33	.27	$.52^{***}$	1560.66	.79	$.19^{***}$
	VEG.sh	347.59	.35	$.10^{***}$	618.43	.67	$.08^{***}$	4674.03	.35	$.59^{***}$	1849.07	.78	$.15^{***}$
	VEG.si	587.20	.32	$.09^{***}$	782.43	.66	$.07^{***}$	5085.91	.32	$.56^{***}$	1920.92	.78	$.13^{***}$
	VEG.tr	698.03	.21	$.07^{***}$	837.88	.64	$.05^{***}$	6401.95	.21	$.46^{***}$	1939.99	.78	$.11^{***}$
climate	PET.co	**133.75**	.06	$.08^{***}$	**72.21**	.65	$.08^{***}$	7924.76	.06	$.24^{***}$	**617.02**	.81	$.20^{***}$
	PET.cv^{log}	611.28	.00	$.06^{***}$	492.36	.66	$.07^{***}$	8472.89	.00	.00	818.55	.81	$.23^{***}$
	PET.ra	**135.01**	.06	$.08^{***}$	**74.06**	.65	$.08^{***}$	7924.51	.06	$.24^{***}$	**618.04**	.81	$.20^{***}$
	PET.sd	436.03	.05	$.06^{***}$	368.48	.64	$.06^{***}$	8060.16	.05	$.21^{***}$	851.86	.81	$.18^{***}$
	PET.sh	472.10	.04	$.06^{***}$	416.52	.64	$.07^{***}$	8089.89	.04	$.21^{***}$	**597.02**	.81	$.20^{***}$
	PET.si	735.01	.03	$.05^{***}$	709.67	.65	$.04^{***}$	8234.94	.03	$.16^{***}$	885.66	.81	$.18^{***}$
	PET.tr^{log}	342.81	.10	$.09^{***}$	290.91	.64	$.09^{***}$	7577.47	.10	$.31^{***}$	1051.40	.80	$.18^{***}$
	PRE.co^{log}	**118.43**	.44	$.10^{***}$	342.73	.65	$.08^{***}$	**3330.45**	.44	$.66^{***}$	**651.14**	.81	$.25^{***}$
	PRE.cv^{log}	954.51	.01	$.03^{***}$	921.86	.63	$.02^{***}$	8342.14	.01	$-.12^{***}$	1609.46	.79	$.13^{***}$
	PRE.ra^{log}	350.94	.47	$.10^{***}$	495.42	.68	$.09^{***}$	**2752.26**	.47	$.69^{***}$	**0.00**	.82	$.31^{***}$
	PRE.sd^{log}	592.87	.46	$.07^{***}$	695.22	.66	$.06^{***}$	**2919.37**	.46	$.68^{***}$	**362.32**	.82	$.29^{***}$
	PRE.sh	465.84	.38	$.06^{***}$	658.83	.63	$.05^{***}$	4249.44	.38	$.61^{***}$	1221.95	.80	$.19^{***}$
	PRE.si	655.94	.44	$.05^{***}$	781.12	.65	$.04^{***}$	**3376.47**	.44	$.66^{***}$	1006.15	.80	$.22^{***}$
	PRE.tr^{log}	**246.41**	.36	$.11^{***}$	348.97	.68	$.10^{***}$	4459.60	.36	$.60^{***}$	**342.65**	.82	$.28^{***}$
	TEM.co	**94.34**	.03	$.09^{***}$	**3.84**	.65	$.09^{***}$	8204.17	.03	$.17^{***}$	943.32	.80	$.18^{***}$
	TEM.cv	345.93	.02	$.06^{***}$	**272.38**	.64	$.06^{***}$	8310.75	.02	$.13^{***}$	1139.63	.80	$.17^{***}$
	TEM.ra	**91.32**	.03	$.09^{***}$	**0.00**	.65	$.09^{***}$	8203.46	.03	$.17^{***}$	942.19	.80	$.18^{***}$
	TEM.sd	317.33	.02	$.06^{***}$	**260.34**	.64	$.06^{***}$	8262.77	.02	$.15^{***}$	1116.08	.80	$.17^{***}$
	TEM.sh	395.97	.01	$.07^{***}$	293.05	.64	$.07^{***}$	8355.95	.01	$.11^{***}$	**742.36**	.81	$.20^{***}$
	TEM.si	666.98	.00	$.05^{***}$	609.73	.64	$.05^{***}$	8435.87	.00	$.06^{***}$	825.69	.81	$.20^{***}$
	TEM.tr^{log}	426.27	.07	$.08^{***}$	378.49	.65	$.08^{***}$	7866.20	.07	$.26^{***}$	1198.75	.80	$.17^{***}$
soil	SOI.co	879.91	.00	$.03^{***}$	856.21	.64	$.03^{***}$	8463.05	.00	$.03^{**}$	1793.05	.79	$.12^{***}$
	SOI.sh	945.14	.00	$.02^{***}$	933.67	.64	$.02^{***}$	8460.09	.00	$.04^{***}$	1834.04	.78	$.10^{***}$
	SOI.si	991.74	.00	$.01^{***}$	977.40	.64	$.01^{***}$	8463.57	.00	$.03^{**}$	1931.03	.78	$.08^{***}$
topography	ELE.co	**92.61**	.03	$.09^{***}$	**3.35**	.65	$.09^{***}$	8184.47	.03	$.18^{***}$	903.34	.81	$.18^{***}$
	ELE.cv	425.74	.04	$.05^{***}$	531.07	.65	$.04^{***}$	8127.20	.04	$.20^{***}$	1548.93	.79	$.13^{***}$
	ELE.ra	**92.10**	.03	$.09^{***}$	**1.40**	.65	$.09^{***}$	8184.50	.03	$.18^{***}$	904.69	.81	$.18^{***}$
	ELE.sd	311.62	.03	$.06^{***}$	**270.80**	.64	$.06^{***}$	8224.60	.03	$.17^{***}$	1072.65	.80	$.17^{***}$
	ELE.sh	330.34	.02	$.08^{***}$	**227.64**	.64	$.08^{***}$	8283.06	.02	$.15^{***}$	**691.73**	.81	$.20^{***}$
	ELE.si	616.35	.01	$.06^{***}$	560.46	.64	$.06^{***}$	8346.47	.01	$.12^{***}$	**814.93**	.81	$.20^{***}$
	ELE.tr^{log}	501.08	.06	$.08^{***}$	468.73	.65	$.08^{***}$	7895.12	.06	$.25^{***}$	1268.42	.80	$.17^{***}$
covariables only					1053.15	.63					2176.51	.78	

Table 4.2 Single- and multi-predictor simultaneous autoregressive (SAR) and ordinary least-squares (OLS) models including environmental heterogeneity (EH) against mammal species richness (222 km × 222 km grain). Multi-predictor models include mean AET, TEM, REG, HII, and one EH measure each (or no EH measure, i.e. *covariables only*). Mammal species richness was square-root transformed, EH measures were log transformed where indicated. Given are ΔAIC, R^2 (pseudo R^2 for the non-spatial term in SAR models, adjusted R^2 for OLS models) and standardised regression coefficient *b* for each model type. Significance levels: *** 0.001, ** 0.01. The ten lowest ΔAIC values per model type are shown in bold. For abbreviations, see Fig. 4.1.

		SAR						OLS					
		single- predictor model			multi- predictor model			single- predictor model			multi- predictor model		
	EH measure	ΔAIC	R^2	b	ΔAIC	R^2	b	ΔAIC	R^2	b	ΔAIC	R^2	b
land cover	GLC.co	486.62	.04	.13***	332.74	.69	.11***	1808.58	.04	.19***	581.51	.77	.20***
	GLC.sh	473.34	.06	.11***	294.66	.71	.10***	1756.02	.06	.25***	474.61	.78	.22***
	GLC.si	496.03	.07	.09***	314.72	.72	.09***	1745.61	.07	.26***	435.95	.79	.23***
	NPP.co	**137.98**	.54	.27***	192.15	.73	.19***	**324.99**	.54	.74***	356.69	.80	.33***
	NPP.cv^{log}	603.78	.14	.01	433.33	.68	.02***	1573.16	.14	−.38***	706.10	.76	−.01
	NPP.ra	205.35	.53	.26***	234.44	.73	.18***	**359.13**	.53	.73***	379.43	.79	.31***
	NPP.sd	223.22	.36	.15***	**82.40**	.73	.13***	979.57	.36	.60***	391.04	.79	.24***
	NPP.sh	241.94	.39	.23***	232.79	.74	.17***	877.57	.39	.63***	286.82	.80	.35***
	NPP.si	384.85	.34	.21***	335.24	.73	.14***	1047.18	.34	.58***	344.79	.80	.36***
	NPP.tr	604.89	.01	.00	434.87	.69	.02***	1862.15	.01	−.10***	665.24	.76	.07***
vegetation	PLA.co	210.04	.61	.52***	283.11	.74	.36***	**0.00**	.61	.78***	451.71	.79	.33***
	VEG.co	288.67	.48	.18***	277.32	.73	.12***	**557.54**	.48	.70***	399.59	.79	.34***
	VEG.cv^{log}	604.77	.02	.00	445.83	.69	.01	1838.20	.02	−.15***	632.28	.77	.10***
	VEG.ma	363.87	.46	.16***	323.66	.72	.10***	**658.24**	.46	.68***	509.02	.78	.28***
	VEG.me	398.74	.33	.19***	390.20	.66	.10***	1095.24	.33	.57***	700.21	.76	−.05**
	VEG.ra	363.87	.46	.16***	323.66	.72	.10***	**658.24**	.46	.68***	509.02	.78	.28***
	VEG.sd	**117.93**	.33	.20***	117.75	.72	.16***	1093.32	.33	.57***	502.65	.78	.25***
	VEG.sh	212.96	.35	.23***	298.47	.69	.14***	1020.49	.35	.59***	663.71	.76	.13***
	VEG.si	358.33	.31	.20***	377.93	.69	.10***	1136.02	.31	.56***	685.45	.76	.09***
	VEG.tr	417.61	.23	.14***	384.02	.70	.08***	1364.76	.23	.48***	657.87	.76	.12***
climate	PET.co	178.18	.08	.16***	**59.35**	.75	.14***	1707.53	.08	.29***	**97.17**	.82	.26***
	PET.cv^{log}	360.43	.00	.13***	195.48	.74	.12***	1883.99	.00	−.01	233.68	.81	.30***
	PET.ra	173.51	.08	.16***	**54.47**	.75	.15***	1707.62	.08	.29***	**97.05**	.82	.26***
	PET.sd	316.04	.05	.11***	191.44	.73	.09***	1784.48	.05	.22***	240.21	.81	.23***
	PET.sh	366.17	.05	.11***	215.03	.74	.10***	1789.53	.05	.21***	**150.40**	.82	.26***
	PET.si	494.45	.02	.07***	335.40	.72	.06***	1845.81	.02	.14***	337.01	.80	.21***
	PET.tr^{log}	307.64	.12	.16***	182.92	.73	.15***	1618.69	.12	.35***	317.07	.80	.22***
	PRE.co^{log}	**0.00**	.56	.22***	**82.01**	.75	.16***	**239.35**	.56	.75***	**79.11**	.82	.36***
	PRE.cv^{log}	453.25	.02	.10***	300.02	.70	.08***	1839.74	.02	−.15***	491.35	.78	.18***
	PRE.ra^{log}	**89.12**	.55	.23***	**107.93**	.76	.18***	**266.83**	.55	.74***	**0.00**	.83	.39***
	PRE.sd^{log}	**145.81**	.54	.20***	162.03	.75	.15***	**336.91**	.54	.73***	**146.94**	.82	.35***
	PRE.sh	**114.28**	.52	.17***	203.52	.71	.11***	**408.42**	.52	.72***	301.78	.80	.29***
	PRE.si	245.88	.56	.15***	278.24	.72	.10***	**221.73**	.56	.75***	280.90	.80	.31***
	PRE.tr^{log}	**21.33**	.42	.24***	**22.81**	.75	.21***	791.86	.42	.65***	**101.94**	.82	.36***
	TEM.co	151.86	.04	.18***	**24.12**	.74	.16***	1794.51	.04	.21***	186.85	.81	.25***
	TEM.cv	288.29	.02	.12***	156.69	.73	.10***	1844.11	.02	.14***	301.36	.80	.23***
	TEM.ra	**150.50**	.04	.18***	**23.22**	.74	.16***	1794.19	.04	.21***	186.12	.81	.25***
	TEM.sd	276.08	.03	.12***	152.13	.73	.10***	1831.71	.03	.16***	292.29	.80	.23***
	TEM.sh	349.80	.01	.12***	177.54	.74	.12***	1866.83	.01	.09***	**163.79**	.82	.27***
	TEM.si	473.81	.00	.08***	305.25	.72	.08***	1884.08	.00	.00	307.98	.80	.25***
	TEM.tr^{log}	317.41	.09	.15***	195.90	.72	.14***	1695.92	.09	.30***	368.55	.80	.22***
soil	SOI.co	479.55	.01	.09***	340.61	.71	.07***	1864.96	.01	.10***	486.36	.78	.19***
	SOI.sh	542.91	.01	.05***	395.35	.69	.04***	1873.56	.00	.07**	571.66	.77	.14***
	SOI.si	573.34	.00	.03***	419.43	.69	.02***	1881.87	.00	.03	627.24	.77	.10***
topography	ELE.co	**114.87**	.05	.19***	**1.36**	.74	.17***	1778.40	.05	.23***	**185.30**	.81	.25***
	ELE.cv	286.19	.05	.10***	239.31	.68	.08***	1787.96	.05	.22***	496.06	.78	.17***
	ELE.ra	**112.42**	.05	.19***	**0.00**	.74	.17***	1778.24	.05	.23***	185.74	.81	.25***
	ELE.sd	238.15	.04	.13***	134.16	.73	.11***	1804.76	.04	.20***	290.37	.80	.22***
	ELE.sh	319.28	.03	.14***	164.28	.74	.13***	1826.29	.03	.17***	**179.00**	.81	.26***
	ELE.si	459.69	.01	.10***	304.16	.73	.09***	1856.49	.01	.12***	309.87	.80	.23***
	ELE.tr^{log}	338.06	.09	.14***	225.45	.72	.13***	1702.99	.09	.29***	399.77	.79	.21***
covariables only					445.38	.68					705.11	.76	

Table 4.3 Single- and multi-predictor simultaneous autoregressive (SAR) and ordinary least-squares (OLS) models including environmental heterogeneity (EH) against mammal species richness (444 km × 444 km grain). Multi-predictor models include mean AET, TEM, REG, HII, and one EH measure each (or no EH measure, i.e. *covariables only*). Mammal species richness was square-root transformed, EH measures were log transformed where indicated. Given are ΔAIC, R^2 (pseudo R^2 for the non-spatial term in SAR models, adjusted R^2 for OLS models) and standardised regression coefficient *b* for each model type. Significance levels: *** 0.001, ** 0.01, * 0.05, †0.1. The ten lowest ΔAIC values per model type are shown in bold. For abbreviations, see Fig. 4.1.

		SAR						OLS					
		single-predictor model			multi-predictor model			single-predictor model			multi-predictor model		
	EH measure	ΔAIC	R^2	b	ΔAIC	R^2	b	ΔAIC	R^2	b	ΔAIC	R^2	b
land cover	GLC.co	76.76	.05	.34***	83.62	.65	.26***	405.21	.04	.22***	151.95	.75	.29***
	GLC.sh	75.54	.09	.28***	79.70	.71	.22***	386.45	.09	.30***	122.36	.77	.29***
	GLC.si	85.90	.10	.26***	80.16	.72	.21***	382.07	.10	.32***	108.71	.78	.31***
	NPP.co	30.84	.58	.34***	59.96	.71	.27***	**80.08**	.58	.76***	85.48	.79	.42***
	NPP.cv^{log}	169.65	.25	−.04	140.66	.69	.05	311.60	.24	−.50***	187.94	.73	−.09†
	NPP.ra	36.98	.56	.32***	61.64	.72	.25***	**93.10**	.56	.75***	88.26	.79	.41***
	NPP.sd	**15.26**	.45	.31***	**13.71**	.77	.27***	183.36	.45	.67***	74.15	.80	.34***
	NPP.sh	29.52	.49	.38***	79.21	.74	.28***	**156.67**	.49	.70***	75.33	.80	.47***
	NPP.si	64.21	.38	.38***	109.81	.71	.23***	234.80	.38	.62***	118.46	.77	.41***
	NPP.tr	168.15	.00	.04†	134.72	.72	.06**	423.49	.00	−.05	163.04	.75	.15***
vegetation	PLA.co	113.08	.58	.49***	119.39	.75	.28***	**78.95**	.58	.76***	141.36	.76	.36***
	VEG.co	112.36	.47	.23***	112.54	.71	.16***	**173.95**	.46	.68***	137.13	.76	.33***
	VEG.cv^{log}	170.90	.13	−.01	140.09	.69	.03†	370.45	.12	−.36***	187.63	.73	.07*
	VEG.ma	123.95	.43	.20***	120.35	.69	.13***	201.67	.43	.65***	170.74	.74	.22***
	VEG.me	151.31	.29	.21***	142.62	.69	.03	287.59	.29	.54***	171.23	.74	−.22***
	VEG.ra	123.95	.43	.20***	120.35	.69	.13***	201.67	.43	.65***	170.74	.74	.22***
	VEG.sd	53.41	.38	.32***	77.79	.72	.24***	230.65	.38	.62***	142.22	.76	.32***
	VEG.sh	90.14	.34	.37***	126.40	.67	.18***	256.48	.34	.59***	191.31	.73	.03
	VEG.si	121.38	.31	.31***	139.58	.69	.09†	274.15	.31	.56***	191.74	.73	.00
	VEG.tr	113.13	.23	.27***	136.25	.69	.10**	317.84	.23	.48***	185.89	.73	.11*
climate	PET.co	**26.14**	.09	.27***	**0.06**	.81	.26***	384.71	.09	.31***	**0.00**	.83	.34***
	PET.cv^{log}	98.44	.01	.23***	77.95	.77	.22***	422.28	.00	−.07	76.17	.80	.40***
	PET.ra	**26.25**	.09	.27***	**0.00**	.81	.26***	384.77	.09	.31***	**0.41**	.83	.34***
	PET.sd	85.32	.03	.19***	76.47	.76	.16***	412.80	.03	.17***	83.56	.79	.26***
	PET.sh	102.80	.02	.17***	80.73	.79	.16***	415.81	.02	.15**	**34.25**	.82	.32***
	PET.si	144.10	.00	.10***	119.90	.74	.09***	424.44	.00	.01	102.73	.78	.26***
	PET.tr^{log}	96.18	.14	.24***	83.23	.77	.22***	363.89	.14	.38***	84.94	.79	.28***
	PRE.co^{log}	**0.00**	.63	.33***	**9.88**	.71	.29***	**25.95**	.63	.79***	**15.28**	.82	.46***
	PRE.cv^{log}	137.20	.04	.16***	83.45	.72	.19***	407.02	.04	−.21***	113.97	.78	.29***
	PRE.ra^{log}	35.05	.60	.30***	**38.16**	.76	.25***	**57.61**	.60	.78***	**25.12**	.82	.44***
	PRE.sd^{log}	45.06	.59	.29***	53.26	.77	.24***	**64.98**	.59	.77***	37.27	.81	.42***
	PRE.sh	**27.29**	.65	.31***	50.89	.79	.25***	**0.00**	.65	.81***	36.15	.82	.44***
	PRE.si	68.74	.65	.28***	88.68	.77	.21***	**4.76**	.65	.81***	58.01	.81	.44***
	PRE.tr^{log}	**20.78**	.45	.34***	**32.66**	.79	.31***	185.80	.45	.67***	36.88	.82	.43***
	TEM.co	**27.33**	.04	.28***	**5.52**	.80	.27***	409.15	.04	.19***	**34.30**	.82	.33***
	TEM.cv	76.77	.01	.21***	67.26	.77	.18***	419.91	.01	.11*	90.30	.79	.27***
	TEM.ra	**27.12**	.04	.28***	**5.26**	.80	.27***	409.13	.04	.19***	**34.01**	.82	.33***
	TEM.sd	75.88	.02	.21***	66.78	.77	.18***	418.09	.01	.13*	87.97	.79	.27***
	TEM.sh	114.07	.00	.18***	85.40	.79	.19***	424.39	.00	−.02	39.27	.81	.38***
	TEM.si	151.11	.02	.10***	122.46	.75	.10***	415.27	.02	−.15**	107.76	.78	.31***
	TEM.tr^{log}	103.28	.10	.22***	88.03	.77	.20***	380.68	.10	.32***	100.94	.78	.27***
soil	SOI.co	119.16	.05	.20***	102.22	.77	.17***	402.88	.05	.23***	62.91	.80	.35***
	SOI.sh	154.05	.02	.08***	127.01	.72	.07***	416.82	.02	.14**	129.53	.77	.22***
	SOI.si	159.02	.00	.05***	129.99	.71	.05***	423.38	.00	.05	161.42	.75	.15***
topography	ELE.co	**27.45**	.06	.29***	**3.81**	.80	.27***	399.15	.06	.25***	**30.12**	.82	.32***
	ELE.cv	118.06	.05	.13***	91.81	.72	.12***	406.09	.04	.21***	134.07	.76	.21***
	ELE.ra	**27.38**	.06	.29***	**4.16**	.80	.27***	399.16	.06	.25***	**30.32**	.82	.32***
	ELE.sd	69.24	.05	.22***	53.95	.78	.19***	403.91	.05	.22***	78.47	.79	.27***
	ELE.sh	112.11	.03	.20***	75.89	.81	.21***	410.65	.03	.18***	**27.94**	.82	.33***
	ELE.si	151.39	.01	.11***	116.62	.77	.12***	419.43	.01	.11*	84.61	.79	.28***
	ELE.tr^{log}	110.19	.10	.20***	96.21	.76	.18***	381.18	.10	.32***	109.63	.78	.26***
covariables only					140.96	.69					189.74	.73	

4.5 Discussion

We compared a wide range of EH measures, revealing differences and similarities in their spatial patterns and their association with global mammal species richness. Besides some redundancies, we detected distinct differences between EH measures based on different variables and calculation methods. We also found a clearly differential importance of EH measures for mammal species richness, indicating that the choice of EH subject area and calculation method strongly influences the outcome of global EH–mammal species richness analyses.

4.5.1 EH measures

Global maps, correlation and principal component analyses revealed some clear differences between EH measures (Figs. 4.1 to 4.3, C.1; Table C.1). For instance, while some areas exhibit low climatic and topographic EH, they may be highly heterogeneous with regard to land cover EH (Fig. 4.2). For some variables, the coefficient of variation (*cv*) was clearly distinct from other calculation methods and yielded negative correlations (Figs. 4.1, C.4; Table C.1), particularly in cases with very low mean values. For instance, NPP and VEG exhibited very low mean values in the Sahara, which resulted in low count (*co*), range(*ra*) or standard deviation (*sd*), but high *cv* values (Fig. C.4). Thus, not all EH measures are redundant but in part cover different aspects of EH, which is not surprising considering its many components and high complexity. Similar results were found in a comparison of topographic slope measures, which showed that different calculation methods and even different resolutions of the underlying digital elevation data can yield widely varying results (Warren et al. 2004).

By contrast, we also detected a close similarity and in part redundancy among some of the EH measures (Figs. 4.1, 4.3, C.4; Table C.1). This makes sense considering that many of the underlying variables are interdependent, e.g. elevation, temperature and potential evapotranspiration. Also a close relationship between vegetation structure and plant diversity, net primary production and land cover classes, as found for some measures in our study, could be expected and confirms previous findings (e.g. MacArthur and MacArthur 1961; Yahdjian and Sala 2006; Kissling et al. 2008; Reu et al. 2011). Higher plant diversity often involves a more complex vegetation structure (MacArthur and MacArthur 1961; Kissling et al. 2008; Qian and Kissling 2010), while NPP and GLC are themselves based, in part, on vegetation types (Global Land Cover 2000 database 2003; Zhao and Running 2010). Vegetation structure may also affect NPP, e.g., by constraining the recovery from drought through the density of meristems (Yahdjian and Sala 2006). Moreover, several calculation methods are closely related, for instance ranges and counts (e.g. elevation range and number of elevation classes), but also other methods like different diversity indices (compare Nøhr and Jørgensen 1997; Fig. 4.1; Table C.1). Similar collinearity and redundancy has also been found for measures of topographic complexity relating to variables such as elevation, slope, or aspect (Bouchet et al. 2014).

4.5.2 EH–richness relationship

The results from our models testing the association between EH measures and mammal species richness also revealed both similarities and great differences among measures. While some EH measures gained almost the same model support and explained the same or very similar amounts of variation in mammal species richness, other measures differed widely in their predictive ability (Tables 4.1 to 4.3). We also detected clear differences in AIC ranks between single- and multi-predictor models. This is because results from single-predictor models or simple correlations may represent indirect effects in addition to direct causal effects (Qian et al. 2009). The decreasing importance of vegetation measures in multi- compared to single-predictor SAR models is most likely due to the inclusion of mean AET as a control variable in multi-predictor models. As shown by PCA, measures of NPP and vegetation EH were particularly associated with the second principal component (Fig. 4.3), which in turn was highly correlated with mean AET. Consistently, several studies have found a close relationship between plant diversity and AET or similar measures of water-energy dynamics (Scheiner and Rey-Benayas 1994; Hawkins et al. 2003a; Kreft and Jetz 2007). It is a well-known predicament that high correlations between plant and animal diversity do not necessarily imply a direct causal relationship but may also arise from both groups depending on the same current and historical environmental conditions (Wolters et al. 2006; Qian and Ricklefs 2008; Jetz et al. 2009). As AET is important for both plant and mammal species richness, it is likely to capture a lot of the explained variation in multi-predictor models that was captured by plant species richness in single-predictor models. The relatively high standardised regression coefficients found in multi-predictor SAR models for AET (median $b = 0.21$) compared to those for EH measures (median $b = 0.07$; see Tab. 4.1) confirms the high importance of water-energy availability for global mammal species richness (Ruggiero and Kitzberger 2004; Qian 2010; Davies et al. 2011). This also goes in line with relatively weak relationships between mammals or birds and vascular plant species richness found in regional and global studies after accounting for environmental variables (Hawkins and Pausas 2004; Jetz et al. 2009). However, the high standardised regression coefficient of PLA even when accounting for AET ($b = 0.46$ compared to b = 0.18 for AET; Table 4.1) still indicates a strong independent role of plant species richness, which confirms other findings (e.g. Qian et al. 2009; Qian and Kissling 2010).

In contrast to vegetation EH, different measures of climatic and topographic EH had high model support in both single- and in multi-predictor models (Table 4.1). This was confirmed by the conditional inference trees of multi-predictor SAR models, which resulted in a significant split between EH subject areas in the first step, generally favouring climatic and topographic EH over land cover, soil, and vegetation EH (Fig. 4.5). The conditional inference trees thereby revealed that the choice of subject area is a more influential methodological decision in macroecological studies on EH–mammal richness relationships than the choice of calculation method. The importance of climatic EH for global mammal species richness goes in line with the high importance of climate *per se* for broad-scale vertebrate richness (Currie 1991; Hawkins et al. 2003a; Field et al. 2009; Hawkins et al. 2012). Topographic EH is likely to gain high model support through its comprehensive role: on one hand, it is a proxy for EH in many conditions, including (micro-)climate, soil, hydrology, and vegetation (Moeslund et al. 2013; Bouchet et al. 2014). On the other hand, topographically heterogeneous areas promote species diversification through isolation and species persistence through the provision of refugia (Hughes and Eastwood 2006; Särkinen et al. 2012). The impact of climatic and topographic EH on species richness may, however, vary between regions in association with other variables such as energy availability, as shown for North American mammals (Kerr and Packer 1997).

By contrast, global mammal species richness is less likely to depend on measures of soil EH, as relatively few species depend directly on specific soil types, e.g. for burrowing (compare Skinner and Chimimba 2005). However, the low support for soil EH measures should also in part be due to the large spatial extent used here, as soil is likely to affect species distributions at smaller spatial scales (Pearson and Dawson 2003). Similarly, many mammal groups are relatively weakly associated with vegetation structure or plant richness at broad spatial scales (Andrews and O'Brien 2000; Jetz et al. 2009), which explains the comparatively low support for vegetation EH in the conditional inference trees. It must also be noted that sample sizes differed widely among subject areas: while we compared 21 measures of climatic EH, we only considered ten measures of vegetation EH and three measures of soil EH. This is because first, not all calculation methods could be applied to the categorical SOI variable, and second, more meaningful variables were available for climatic EH at global extent.

We also detected differences in model support among calculation methods (Figs. 4.4, 4.5). According to conditional inference trees, *co* and *ra* measures, which are among the most frequent EH measures in the literature (Stein and Kreft 2014), consistently received higher model support across spatial grains. By contrast, particularly *cv*, Simpson index (*si*) and terrain ruggedness index (*tr*) were associated with larger ΔAIC values (Fig. 4.5). As already noted, at the global extent used in this study, regions with low mean values, e.g. in VEG or NPP, featured very high *cv* values and *vice versa.* The associated EH measures may therefore represent artefacts of the particular calculation method rather than meaningful proxies of EH. However, for other variables and at smaller spatial extents, *cv* measures have been used successfully in different studies. Vertebrate richness in Wyoming, for example, exhibited both higher and lower correlation coefficients with *cv* compared to *ra* EH measures depending on the associated variables and spatial grains (Fraser 1998). In New Mexico, bird species richness was particularly strongly associated with *cv* of elevation (St-Louis et al. 2006). Likewise, relatively strong associations compared to other measures were found between variants of the Simpson index of different variables and species richness of plants (Kumar et al. 2006) and birds, amphibians, reptiles, and butterflies (Ricklefs and Lovette 1999). However, these results in part depended on spatial scale, which was also much smaller than in the current study. By contrast, a study from Singapore reported a lack of significant correlations between inverse Simpson index of habitat types and species richness of vascular plants, butterflies, and birds (Koh et al. 2002). The authors hypothesized that this was due to the resolution of the underlying data, such that diversity in microhabitats could not be adequately represented by their measure. Overall, these contrasting results confirm the high complexity of EH–richness relationships, which highly depend on the study systems at hand, including spatial scales, taxa, and taxon-specific environmental variables. Even the shape of EH–richness relationships may vary depending on EH measures, habitat types, and spatial scales (Bar-Massada and Wood 2014). Hence, it seems advisable to consider different measures in EH research and to choose them carefully with regard to the system of interest.

Our study included all terrestrial mammals, and it is likely that our conclusions would differ when analysing separate mammal groups. For instance, soil EH should be more important for fossorial mammals, whereas vegetation EH should affect arboreal, frugivorous and herbivorous mammals more than, e.g., carnivores. Consistently, small arboreal frugivores and insectivores in southern Africa were much more strongly correlated with woody plant species richness than large or fossorial mammals (Andrews and O'Brien 2000). Another study based on the same dataset also found ground-living, climbing, and aerial mammals to be closely related to woody plant species richness after accounting for environmental variation, in contrast to fossorial and aquatic (i.e. specialised for swimming) mammals (Qian et al. 2009). However, the same study surprisingly detected only minor differences in the importance of plant richness for different trophic guilds, i.e. herbivores versus insectivores, carnivores, and omnivores. The authors attributed this to spatial grain, which again highlights the pervasive impact of spatial scale in environment–richness research.

Spatial scale A distinct outcome of this study was the clearly differential importance of EH subject areas for global mammal species richness. However, it is likely that the presented patterns will be different at spatial grains and extents other than the ones analysed here. EH in different environmental variables becomes apparent at different spatial scales, and also the importance for species richness varies with scale (Rahbek and Graves 2001; Whittaker et al. 2001; Kent et al. 2011). For instance, a study confined to Wyoming found climatic and topographic EH to be less important for vertebrate richness than land cover and vegetation EH (Fraser 1998). The effect of topographic EH was furthermore thought to affect species richness indirectly through the vegetation. We generally expect climatic and topographic EH to become less important and vegetation EH to become more important at smaller scales, where biotic interactions play a larger role (Whittaker and Field 2000; Rahbek and Graves 2001; Field et al. 2009; Kent et al. 2011). At the local scale, vegetation structure has been found to be highly correlated with species richness of small Australian mammals (Willis and Whittaker 2002). Also plant species richness was shown to be important for mammals in Australia, southern Africa and China (Qian et al. 2009; Qian and Kissling 2010; Garden et al. 2010), even when accounting for climatic conditions. These associations between vegetation EH and mammal richness can be explained by a larger variety of resources, shelter, and nesting sites in areas with more complex and species-rich vegetation (Hutchinson 1959; Garden et al. 2010; Qian and Kissling 2010). Consistently, a global meta-analysis found vegetation and topographic EH to be most strongly associated with terrestrial plant and animal species richness overall (Stein et al. 2014), however, the analysis covered multiple spatial grains and extents. Although we included different spatial grains in our analysis, the underlying data did not allow us to consider finer grains than the ones used here. The global scale of our study also impeded a meaningful comparison of different spatial extents, as smaller extents would have biased the analyses with regard to the spatial distribution of EH (compare Fig. 4.2). However, previous studies have stressed the importance of spatial extent for outcomes of species-richness research (Davies et al. 2007; Whittaker et al. 2007), therefore our results should be considered against the background of the global extent used here.

Multi-predictor models revealed an increasing trend in variance explained by EH with spatial grain, which is consistent with findings of Fraser (1998). A recent global meta-analysis also found that larger spatial grains are generally associated with stronger EH–richness relationships (Stein et al. 2014). This is likely due to the fact that larger grain size usually entails larger within-cell variability in EH (Fraser 1998; van Rensburg et al. 2002). Also, allopatric speciation and species turnover mediated by EH should become more important with larger spatial grain. Finally, adverse fragmentation effects associated with high EH may be more significant at small spatial scales (Tamme et al. 2010; Laanisto et al. 2013).

4.6 Conclusions

We showed that while there is a considerable amount of collinearity and redundancy among the 51 EH measures analysed here, there are also clear differences among measures and regions. Different measures thus represent various aspects of EH that should influence species richness through different mechanisms related to coexistence, persistence, and diversification. Climatic and topographic EH as well as count and range measures, which are in fact already among the most widely used measures at broad spatial scales, generally received highest model support for explaining mammal species richness at the global extent considered here. At smaller spatial scales and for particular functional mammal groups, results are likely to differ and will be interesting to investigate in future studies.

Although we calculated a great number of relatively easily available EH measures, other measures such as more detailed indices of land cover and topographic EH or vegetation structure could be computed (e.g. McGarigal and Marks 1994; McElhinny et al. 2005; Olaya 2009; Bouchet et al. 2014), which may be more informative about the underlying processes. Data availability for many of these measures such as foliage height diversity is so far limited to small spatial scales, but further advancements of remote sensing techniques will hopefully allow the calculation of broad-scale measures of vegetation structure in the future (e.g. Goetz et al. 2010; Hall et al. 2011). While different EH measures often represent different processes influencing species richness, it is hard to actually identify the mechanisms underlying EH–richness relationships. Choosing measures that reflect the actual function of environmental variables, e.g. measures representing effects of topographic EH on insolation or moisture, should promote our understanding of the diverging relative importance of EH measures in species-richness studies (Moeslund et al. 2013).

EH is a very diverse and complex topic, and we showed how sensitive the results of EH–richness studies are to the particular calculation method, variable, and statistical approach, and thereby to the ecological aspects underlying EH measures. Here we were interested in a methodological comparison and thus included many different EH measures. As methodological decisions significantly influence study outcomes, EH measures and statistical methods in single case studies should be chosen carefully according to a particular hypothesis that considers the taxon, spatial scale, study system, and mechanism of interest. A selective comparison of multiple EH measures should promote conclusions and generalisations about the role of EH for species richness.

[F]reedom of thought is best promoted by the gradual illumination of men's minds, which follows from the advance of science.

Charles Darwin

5

Synopsis

Introduction Spatial environmental heterogeneity (EH) is considered to be one of the most important factors determining species richness patterns worldwide (Tews et al. 2004; Field et al. 2009). Early research revealed a positive relationship between vegetation structure and bird species diversity (MacArthur and MacArthur 1961) and lizard species richness (Pianka 1967). A close positive relationship between area, EH, and species richness was also recognized early (Hamilton et al. 1963; Williams 1964). Since then, an ever growing number of studies on the topic has been published. However, in addition to positive EH–species richness relationships, negative, hump-shaped, and non-significant relationships have also been found (e.g. August 1983; Tamme et al. 2010; Allouche et al. 2012; Gazol et al. 2013). Therefore, even though ecological theory predicts a positive effect of EH on species richness, the generality of positive EH–richness relationships in nature is still debated.

Positive relationships between EH and species richness have been attributed to three major 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; Currie 1991). Second, increased EH is expected to enhance species persistence through the increased provision of shelter, e.g. from predators, cold or insolation, and of refuges from long-lasting adverse environmental conditions, like glaciations (Garden et al. 2010; Kallimanis et al. 2010). Finally, EH should increase the probability of species diversification through isolation or adaptation to diverse environmental conditions (Andrews and O'Brien 2000; Givnish 2010). Negative EH–richness relationships are mainly thought to result from unfavourable fragmentation effects (Tamme et al. 2010; Fahrig et al. 2011). Alternatively, negative relationships could be caused by an area–heterogeneity trade-off (Kadmon and Allouche 2007; Allouche et al. 2012; Bar-Massada and Wood 2014), i.e. a reduction in the area of individual habitat types associated with increasing heterogeneity. EH might therefore increase the possibility of stochastic extinctions, as smaller areas can only support smaller population sizes (but see Carnicer et al. 2013; Hortal et al. 2013). Unsurprisingly, considering the range of mechanisms thought to drive it, the relationship between EH and species richness is highly complex, and difficult to quantify and comprehend.

The difficulty of understanding EH–richness relationships also arises from the considerable variability in EH–richness research. Studies have not only encompassed many different taxa, ecosystems, and spatial scales, but have measured EH itself in numerous different ways. For instance, EH has been quantified with regard to vegetation structure, plant diversity, topographical complexity, and diversity of habitat types. It has also been quantified with many different measures, based on a variety of 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 to understand whether different authors refer to the same thing (McCoy and Bell 1991). Thus, the variability in EH–richness research hampers the finding and comparison of studies and thereby our understanding of the general EH–richness relationship.

Several reviews have treated EH–diversity relationships (e.g. Tews et al. 2004; Field et al. 2009; Hortal et al. 2009; Lundholm 2009; Tamme et al. 2010). However, general conclusions from these reviews are limited because not all of them are quantitative, and most focus on only a single component of EH and/or consider only plants or animals. The overall aim of this thesis was therefore to examine the concept and role of EH within a wider, 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 and systematic review of the EH–richness literature, covering all studies that analysed the relationship between EH and species richness of terrestrial plants or animals at landscape ($\geq$ 10 km^2) to global extents. In chapter 2, I scrutinised the methodology and terminology used in EH–richness research based on a dataset of 192 studies including 1148 data points (Stein and Kreft 2014). Specifically, I investigated how EH has been quantified and termed and whether the generally indistinct terminology could be clarified by analysing its association with quantification methods. Furthermore, I classified the resulting EH measures by subject area, such as vegetation or topography, and calculation method, such as range or standard deviation. I used this classification to study trends in research and later, in chapter 3, to analyse differences in the strength of EH–richness relationships between different measures. I summarised which taxa, regions, habitat types, and spatial scales have been most studied and identified sources of bias and research gaps. Furthermore, I reviewed the mechanisms thought to underlie positive EH–richness relationships and linked them to the studied EH subject areas and other study characteristics, such as taxon and spatial scale.

In chapter 3, I then examined the strength and direction of EH–richness relationships across terrestrial study systems worldwide using meta-analytic techniques (Stein et al. 2014). I tested whether the relationship is positive overall, and whether it differs among EH measures. Moreover, I analysed whether there are differences in the EH–richness relationship between study taxa, habitat types, and spatial scales. Based on the insights from chapters 2 and 3, I computed a range of EH measures for all land areas worldwide in chapter 4 and investigated differences and similarities among these measures and their spatial patterns. I also tested to what extent different measures vary in their relationship with species richness of terrestrial mammals. I was particularly interested in whether the level of model support of these relationships depended more on the subject area or calculation method of EH measures.

Methods The systematic review and meta-analysis (chapters 2 and 3) were based on an extensive formal literature search that comprised three different strategies. First, I used a comprehensive keyword search in *ISI Web of Science*, combining terms like "species diversity" or "species richness" with 68 different terms for EH, such as "habitat heterogeneity" or "structural complexity" (see Appendix A.1 for the complete search string). Second, I reviewed the studies cited in several review articles (Ricklefs and Lovette 1999; Tews et al. 2004; Field et al. 2009; Hortal et al. 2009; Lundholm 2009; Tamme et al. 2010). Third, I screened the reference lists of the studies detected in the first two steps. Finally, I reviewed the 2236 articles found to decide whether they conformed with a set of inclusion criteria. I included only observational studies that reported on the relationship between a quantitative measure of spatial EH and the number of plant or animal species in terrestrial systems from landscape to global extents. Moreover, studies had to contain statistics or raw data that could be converted to Fisher's z, i.e. the effect size used in the meta-analysis.

To address the research questions of chapter 2, I recorded the measures and terms used for EH in each study as well as the potential mechanisms behind EH–richness relationships that were addressed. I classified EH measures according to subject area and calculation method and also collected information on study taxon, location, habitat type, data source and type, and spatial grain and extent.

For the meta-analysis (chapter 3) I additionally recorded whether each analysis was based on equal-area study units or not. As many studies contributed multiple data points, these were not statistically independent. To account for this, we used a novel technique based on robust variance estimation (Hedges et al. 2010) that allows the combination of dependent effect size estimates in a single analysis. To our knowledge, our study (Stein et al. 2014) is the first ecological meta-analysis to use this method. To quantify the strength and direction of the EH–richness relationship, I estimated a mean effect size weighted by sample size for the complete dataset. I then used mixed-effects meta-regression to determine whether the strength of the relationship differed between EH components and whether it was influenced by particular study-level covariates, such as taxon, habitat type and spatial scale.

For chapter 4, I used the subject areas and calculation methods identified in chapter 2 to develop a set of 51 EH measures and quantify them over the terrestrial surface of the globe. I used mostly publicly available environmental datasets to derive measures of land cover EH (land cover classes and NPP; Global Land Cover 2000 database 2003; Zhao and Running 2010), vegetation EH (vascular plant species richness and canopy height; Kreft and Jetz 2007; Simard et al. 2011), climatic EH (annual precipitation, temperature and potential evapotranspiration; Hijmans et al. 2005; Trabucco and Zomer 2009), soil EH (major soil groups; FAO/IIASA/ISRIC/ISSCAS/JRC 2012), and topographic EH (elevation; Hijmans et al. 2005). To compare calculation methods, I computed the count, Shannon entropy, Simpson index, coefficient of variation, standard deviation, range, terrain ruggedness index (Wilson et al. 2007), mean, and maximum of all nine environmental variables, where feasible. I analysed the variability in EH measures using correlation and principal component analysis (PCA) and illustrated regional differences in EH with global maps of single EH measures and multidimensional EH space based on the PCA. I then examined the relationship between each measure and mammal species richness (derived from the IUCN mammal assessment; IUCN 2013) with ordinary least squares (OLS) regression and simultaneous autoregressive (SAR) models that accounted for spatial autocorrelation in OLS model residuals. I compared single-predictor models including one EH measure each with multi-predictor models that additionally accounted for current climate (actual evapotranspiration (Ahn and Tateishi 1994) and mean annual temperature), biogeographic regions (Kreft and Jetz 2010) and human influence index (Wildlife Conservation Society - WCS, and Center for International Earth Science Information Network - CIESIN - Columbia University 2005). As EH–richness relationships are scale-dependent (Rahbek and Graves 2001; Tamme et al. 2010), as demonstrated in chapter 3, I repeated the analyses across three different grain sizes (12,364 km^2, 49,457 km^2, and 197,829 km^2), while keeping the area of study units constant. I then compared the association of EH measures with species richness based on the Akaike Information Criterion (AIC) of SAR models. As several measures were highly correlated, I did not concentrate on the exact AIC ranks of particular measures. Instead, I computed conditional inference trees (Hothorn et al. 2006) to examine whether EH subject areas or calculation methods were more important for model support.

Results and discussion The literature review in this thesis is the first, to my knowledge, that systematically quantifies terminology and mechanisms associated with EH measurement. In chapter 2, I revealed how heterogeneous and ambiguous the quantification and terminology of EH have been. Overall, 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. To promote understanding, synthesis, and thereby advancement in EH–richness research, authors should choose unambiguous terms and measure names and avoid unnecessary use of synonyms. 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 adopted the term environmental heterogeneity as a general umbrella term, as "environmental" is much more comprehensive and less ambiguous than "habitat" (Triantis et al. 2003), and because heterogeneity, in contrast to diversity, may involve both within- and between-habitat variability (Nilsson et al. 1988).

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 this thesis, studies on climatic and soil EH were clearly underrepresented (associated with 11 and 12 EH measures, respectively) in comparison to land cover, vegetation, and topographic EH (quantified by 18, 54, and 65 measures, respectively). As different EH measures cover different aspects of EH, the comparison of various EH measures in species-richness studies should allow more detailed insights into the EH–richness relationship. Chapter 2 furthermore revealed a clear 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 insight into the generalisability of our current knowledge. Moreover, while many studies compared multiple EH measures, taxa, or spatial scales, focused reanalysis of existing datasets and future comparative studies—preferably large-scale collaborative research projects (Borer et al. 2014)—should deepen our understanding of taxon- and scale-dependent effects of EH, e.g. with regard to functional groups.

I detected seven mechanisms that were used in the literature to explain positive effects of EH on species richness. The majority of studies referred to niche theory (Hutchinson 1959), i.e. more diverse resources and increased niche space allowing more species to coexist. These studies mostly investigated vegetation EH, whereas studies addressing evolutionary mechanisms mostly quantified topographic EH. In this context, higher topographic EH is thought to increase the probability of diversification through isolation and diverse adaptation (Simpson 1964; Ruggiero and Hawkins 2008). The association between mechanism of interest and EH measure used may be another explanation for conflicting conclusions regarding EH–species richness relationships.

In the quantitative meta-analysis of the same dataset (chapter 3), I revealed that the EH–richness relationship is significantly positive overall, 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. The meta-regressions revealed that the use of equal-area study units, spatial grain, and spatial extent clearly influence the strength of EH–richness relationships, at least for the analysed 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 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. This 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 likely 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 necessary to consider spatial scale in EH–richness studies, and researchers should compare multiple spatial grains and extents, if possible, and, more importantly, keep the area of study units constant. Despite the comprehensive dataset, several questions remained unanswered because many studies had to be excluded and not enough data points were available for all combinations of study characteristics. 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. To foster synthesis in this regard, it is crucial that authors provide all necessary study characteristics and statistics, even for non-significant relationships (Hillebrand and Gurevitch 2013).

In chapter 4, I revealed clear differences, but also similarities, among the 51 EH measures and their spatial patterns. Several EH measures were surprisingly weakly correlated, and particularly the coefficient of variation showed distinct patterns from the rest. Other EH measures were highly correlated, which is not surprising considering the close associations among 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 small distances (Körner 2000; Moeslund et al. 2013). I also identified strong 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-east Asia featured high vegetation EH. I found that measures of climatic and topographic EH and count and range measures generally received highest model support in explaining global terrestrial mammal species richness, when current climate, regional effects and human influence were accounted for. Coefficient of variation, Simpson index and terrain ruggedness index generally received lower support across all spatial grains I studied, although these measures have successfully been used at smaller spatial scales (e.g. Fraser 1998; Kumar et al. 2006). It is reassuring that some of the most easily available and therefore most frequently used measures in the literature, e.g. elevation range, received good support. However, generalisations to smaller spatial scales and other taxa, such as specialised habitat or trophic groups, should be done carefully, as different patterns are to be expected.

The results from chapters 3 and 4 partly corresponded; for instance, both chapters revealed a high importance of topographic EH for species richness. However, conclusions about the relative importance of climatic and vegetation EH differed. This can in part be explained by the fact that the meta-analysis generalised over many different taxa, while the case study focused on mammals. As the impact of EH depends on taxon-specific characteristics such as body size, range size, thermoregulation, trophic guild, habitat preferences and motility, differences among groups are expected, even though taxonomic group showed no significant effect in meta-regressions. Moreover, studies on climatic EH were underrespresented in the dataset that was the basis for the meta-analysis. Therefore, more comparative studies including various components of EH that represent different mechanisms should help us to better understand the relative importance of the five subject areas.

Conclusions and outlook Spatial environmental heterogeneity has fascinated researchers for centuries, playing a role in such different fields as ecology, biogeography, conservation biology, and evolution. The present thesis provides an unprecedentedly comprehensive assessment of the measurement and terminology of EH in both biotic and abiotic conditions, including a quantitative investigation 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. I hope that my work in this regard will prove useful and propose that the terminology used in this thesis be adopted in future research. Unambiguous terms, clear definitions, and the avoidance of unnecessary synonyms should foster the understanding, comparison, and synthesis of studies and thereby promote the advancement of this field. Using novel meta-analytical techniques and a large dataset, 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 all future EH–richness studies.

The findings from all chapters of this thesis agree that EH is a complex and context-dependent topic, whose quantification methods greatly influence study outcomes. While some of the most common EH measures received high model support in the case study (chapter 4), many more measures have been developed (compare e.g. chapter 2; McGarigal and Marks 1994; McElhinny et al. 2005; Olaya 2009; Bouchet et al. 2014), and different measures are most appropriate for different study systems. EH measures should be chosen according to the specific mechanism of interest, and with regard to the taxon, ecosystem, spatial grain, and spatial extent 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. As 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 are crucial for further advancement of this field.

Mechanistic interpretations were relatively rare in the present literature dataset, echoing previous reports of missing links between theories and data in the ecological literature in general (Scheiner 2013). Compared with mechanisms related to the promotion of species coexistence, mechanisms linked with species persistence and diversification were clearly underrepresented. 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.

This study mainly focused on linear EH–richness relationships, but the existence of non-linear relationships involving hump-shaped or saturation curves has also been suggested (e.g. Seto et al. 2004; Kadmon and Allouche 2007; Marini et al. 2008, 2011; Allouche et al. 2012). Investigation of non-linearities through methods like generalised additive modelling in future research is likely to promote our understanding of the interrelationship between EH and other determinants of species richness that may explain such non-linearities, for instance area or productivity. Insights into the actual shape of EH–richness relationships and its determinants should thereby also help validate the generality of the area–heterogeneity trade-off hypothesis. Other factors like energy availability have also been shown to influence the association between EH and species richness (Kerr and Packer 1997; Kreft and Jetz 2007). However, as this could not be confirmed by the meta-analysis, the exact interplay between energy, EH, and species richness should be investigated further in future studies.

Despite the considerable advancements made in the field of EH–richness relationships with this thesis, many gaps in our understanding still remain. In particular, more studies are needed in the tropics, on invertebrates and other microfauna and flora, with soil measures, considering multiple spatial scales, and with more complex statistical approaches including non-linearity. But with the new, solid foundation for further research provided by my work in this thesis, it will hopefully not be long before the question of how EH affects species richness is thoroughly understood.

Appendices

A
Supporting information to chapter 2

A.1 Literature search in *Web of Science*

Our extensive keyword search in *Web of Science* included all document types and languages up to the 19th of April 2011. Using the *topic* field, our search covered titles, abstracts, author keywords, and "Keywords Plus". The latter include frequent words from the titles of the articles cited by a given article. Although the search results included many irrelevant articles, insufficiencies in our keyword search string should have been counteracted by this comprehensive search mode.

We used the following search terms (split into two searches because the number of terms per search was restricted):

> ts=("habitat heterogeneity" OR "habitat diversity" OR "habitat complexity" OR "habitat number" OR "biotop$$ heterogeneity" OR "biotop$$ diversity" OR "biotop$$ complexity" OR "biotop$$ number" OR "ecotop$$ heterogeneity" OR "ecotop$$ diversity" OR "ecotop$$ complexity" OR "ecotop$$ number" OR "biom$$ heterogeneity" OR "biom$$ diversity" OR "biom$$ complexity" OR "biom$$ number" OR "structural heterogeneity" OR "structural diversity" OR "structural complexity" OR "spatial heterogeneity" OR "spatial complexity" OR "topograph* heterogeneity" OR "topograph* diversity" OR "topograph* complexity" OR "relief heterogeneity" OR "relief diversity" OR "relief complexity" OR "aspect heterogeneity" OR "aspect diversity" OR "aspect complexity" OR "architectur$$ heterogeneity" OR "architectur$$ diversity" OR "architectur$$ complexity" OR "land use heterogeneity" OR "land use diversity" OR "land use complexity" OR "altitud* heterogeneity" OR "altitud* complexity" OR "elevation$$ heterogeneity" OR "elevation$$ complexity" OR "environment$$ heterogeneity" OR "environment$$ diversity" OR "environment$$ complexity" OR "climat$$ heterogeneity" OR "climat$$ diversity" OR "climat$$ complexity" OR "soil heterogeneity" OR "soil complexity" OR "foliage heterogeneity" OR "foliage diversity" OR "foliage complexity" OR "foliage height heterogeneity" OR "foliage height diversity" OR "foliage height complexity" OR "vegetation$$ heterogeneity" OR "vegetation$$ diversity" OR "vegetation$$ complexity" OR "NDVI" OR "normalized difference vegetation index" OR "geoheterogeneity" OR "geodiversity" OR "geocomplexity" OR "geograph* heterogeneity" OR "geograph* diversity" OR "geograph* complexity" OR "landscape heterogeneity" OR "landscape diversity" OR "landscape complexity") AND ts=("species diversity" OR "species richness" OR "species number" OR "species density").

As we aimed at avoiding taxonomic bias in our keywords, we searched for "species" only and not for particular taxa, such as "bird" or "arthropod diversity". This keyword search resulted in more than 2,600 articles, which we refined by excluding the following subject areas and keywords:

> (MARINE & FRESHWATER BIOLOGY OR WATER RESOURCES OR OCEANOGRAPHY OR MICROBIOLOGY OR PALEONTOLOGY OR MYCOLOGY OR FISHERIES OR BIOCHEMISTRY & MOLECULAR BIOLOGY OR BIOTECHNOLOGY & APPLIED MICROBIOLOGY OR LIMNOLOGY); NOT ts=(fish* OR marine OR aquatic OR macrobenthos OR macrobenthic OR benthic OR benthos OR pelagic OR pelago OR diatom* OR plankton* OR zooplankton* OR phytoplankton* OR nekton* OR coral$ OR "coral reef$" OR "deep sea" OR seafloor OR "sea floor" OR bivalv* OR alga OR algae OR mussel$); NOT ts=(bacteri* OR virus* OR viral OR archaea* OR microbe* OR microbiol* OR microbial* OR mycolog* OR fungus OR fungi OR fungal).

This left 1,732 studies. We checked the titles, abstracts and in many cases the complete article to determine if each study was relevant and matched our inclusion criteria.

A.2 References to studies included in the review and in appendix A.3

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A.3 Measures and measure variants of environmental heterogeneity

Table A.2 Measures and measure variants of environmental heterogeneity (EH) occurring in 192 studies listed in Appendix A.2. Measures are sorted by EH subject area and grouped into thematic categories based on [1] and [2]. Terms are those terms for EH that were used in combination with at least one of the given measures per row. Note that we included the number of insect species, which occurred in one study, in the measure category *species diversity*. Although this measure is not formally part of vegetation EH, it was closely related to the number of plant species in the respective study [122] and represents the same mechanisms related to resource diversity, which is why we included it here. Abbreviations: CA, correspondence analysis; CV, coefficient of variation; DBH, diameter at breast height; GLCM, grey level co-occurrence matrix; MDS, multidimensional scaling; NDVI, normalized difference vegetation index; PCA, principal component analysis; PET, potential evapotranspiration; SD, standard deviation.

Subject area	Measure category	Measures	Measure variants	Terms	References
climate	composite measure	size-adjusted habitat volume	size-adjusted habitat volume (ordination based on climatic variables)	habitat heterogeneity	[3]
climate	energy variation	CV of solar radiation; CV of temperature; index of temperature variation; range of PET; range of solar radiation; range of temperature	CV of insolation; CV of irradiance; CV of temperature; index of temperature variation; range of PET; range of solar radiation; range of temperature	environmental diversity; environmental heterogeneity; environmental variation; habitat diversity; habitat heterogeneity; variation	[4–12]
climate	water variation	CV of precipitation; index of precipitable water variation; index of relative humidity variation; range of precipitation	CV of precipitation; index of precipitable water variation; index of relative humidity variation; range of precipitation	environmental heterogeneity; environmental variability; habitat diversity; habitat heterogeneity; variation	[4–5, 7–9, 13]
hetmixed	composite measure	composite heterogeneity index; environmental heterogeneity index; number of ecological variables present	composite heterogeneity index; environmental heterogeneity index; number of ecological variables present	environmental heterogeneity; habitat diversity	[14–16]
land cover	area (class metric)	area of forest cover; CV of percentage of forest cover; percentage of cover of agricultural land; percentage of cover of forest or woodland; percentage of cover of grassland; percentage of cover of non-arable area; percentage of cover of semi-natural habitat; percentage of cover of shrubland; range of forest density (in % forest cover)	CV of forest density (in % forest cover); forest cover (area); percentage of arable land; percentage of deciduous vegetation; percentage of forest and rural habitat; percentage of forest cover; percentage of grassland cover (inverse measure); percentage of grassland cover (positive measure); percentage of non-arable area; percentage of pasture land; percentage of sagebush vegetation in matrix; percentage of semi-natural habitat; percentage of shrubland cover; percentage of woody vegetation cover; range of forest density (in % forest cover)	environmental heterogeneity; habitat heterogeneity; habitat structure; land cover complexity; land use heterogeneity; landscape characteristics; landscape complexity; landscape composition; landscape features; landscape heterogeneity; landscape matrix; landscape structure; spatial heterogeneity; vegetation heterogeneity	[8, 17–34]
land cover	composite measure	ordination of habitat variables	factor analysis of habitat diversity; first axis of PCA of habitat variables	habitat diversity	[35–36]

Table A.2 continued

Subject area	Measure category	Measures	Measure variants	Terms	References
land cover	diversity (landscape metric)	chorological complexity of landscape classes; CV of NDVI; degree of forest fragmentation; density of land cover types; evenness of land cover types; Gini–Simpson index of patch types; Hill abundance of landscape classes; inverse Simpson index of land cover types; jack-knife estimate of land cover types; McIntosh diversity of landscape classes; McIntosh dominance of landscape classes; mean angular-second moment of GLCM of a moving window; mean contrast of GLCM of a moving window; mean correlation of GLCM of a moving window; mean entropy of GLCM of a moving window; mean Euclidian distance in ordination of spectral data; mean information measure of correlation of GLCM of a moving window; mean sums of squares variance of GLCM of a moving window; number of land cover types; number of microhabitat types; range of grey-tone values of spectral data; range of NDVI; relative landscape richness; scores of number of land cover types; SD of entropy of GLCM of moving window; SD of NDVI; SD of spectral data; Shannon index of land cover types; Turner dominance of landscape classes; typological complexity of landscape classes	chorological complexity of landscape classes; CV of July NDVI; degree of forest fragmentation; density of land cover types; evenness of land cover types (area proportion); evenness of landscape classes (number of polygons); evenness of vegetation types; Gini–Simpson index of patch types; Hill abundance of landscape classes; inverse Simpson index for ground cover class's patches; inverse Simpson index for ground cover classes or patch types; inverse Simpson index for habitat diversity; inverse Simpson index for habitat diversity (proportion of trap stations); jack-knife estimate of the number of habitat types; McIntosh diversity of landscape classes; McIntosh dominance of landscape classes; mean angular-second moment of GLCM of a moving window; mean contrast of GLCM of a moving window; mean correlation of GLCM of a moving window; mean entropy of GLCM of a moving window; mean Euclidian distance in ordination of spectral data; mean information measure of correlation of GLCM of a moving window; mean range of grey-tone value in a moving window; mean SD of mean grey-tone value in a moving window; mean sums of squares variance of GLCM of a moving window; modified Shannon index of land use classes; number of ecosystem types; number of ecotope types; number of habitat types; number of land cover types; number of microhabitat types; number of plant community types; number of primary cover types; number of seasonal land cover types; number of unique combinations of primary and secondary cover types; number of vegetation formations; number of vegetation types; range of July NDVI; range of NDVI; relative landscape richness; scores of number of land cover types; SD of entropy of GLCM of moving window; SD of NDVI; SD of spectral reflectance; Shannon index of forest site types; Shannon index of habitat types; Shannon index of land cover classes; Shannon index of land use classes; Shannon index of landscape classes ($\log_2$); Shannon index of vegetation types; Turner dominance of landscape classes; typological complexity of landscape classes	biotope diversity; biotope heterogeneity; ecosystem diversity; ecotope diversity; environmental diversity; environmental heterogeneity; environmental variability; geoecological heterogeneity; habitat complexity; habitat diversity; habitat heterogeneity; habitat richness; habitat structure; land cover complexity; land cover heterogeneity; land cover variety; land use diversity; landscape complexity; landscape diversity; landscape heterogeneity; landscape structure; microhabitat diversity; patch diversity; spatial heterogeneity; spatial variation; spectral heterogeneity; spectral variation; vegetation heterogeneity; vegetation structure	[8, 13–14, 17, 20–21, 23, 26–27, 30, 33, 37–102]
land cover	edge (class/landscape metric)	edge density; interspersion and juxtaposition index; mean patch edge; proportion of edges; sum of all edges	edge density; interspersion and juxtaposition index (per cent); mean patch edge; proportion of edges; sum of all edges	habitat heterogeneity; landscape heterogeneity; landscape structure; spatial heterogeneity	[26–27, 67, 103–104]
land cover	patch density, size, and variability (class/landscape metric)	mean patch size of a land cover type; number of land cover patches; SD of patch size	mean patch size; mean patch size of coniferous vegetation; mean patch size of deciduous vegetation; mean patch size of forest habitat; mean patch size of shrubland (positive measure); number of ecotope patches (irrespective of ecotope type); number of habitat patches (irrespective of habitat type); SD of patch size	ecotope diversity; habitat heterogeneity; landscape configuration; landscape heterogeneity; landscape structure; spatial heterogeneity	[24, 26, 33, 67, 102–103]
land cover	shape (class/landscape metric)	mean number of shape characteristic points; mean shape index; minimum bounding rectangle ratio; number of shape characteristic points; patch fractal dimension; perimeter–area ratio	area weighted mean number of shape characteristic points; area weighted mean of minimum bounding rectancle ratio; area weighted mean patch fractal dimension; area weighted mean shape index; double log fractal dimension; mean patch fractal dimension; mean perimeter–area ratio; mean shape index; perimeter–area ratio (of a whole landscape); sum of number of shape characteristic points; sum over minimum bounding rectancle/area ratio	habitat diversity; land cover heterogeneity; landscape complexity; landscape heterogeneity; shape complexity	[23, 103, 105]
soil	diversity of soil or substrate types	number of substrate types; scores of number and percentage of soil types; Shannon index of soil types	number of geological substrata; number of soil types; scores of number and percentage of soil types; Shannon index of soil and geomorphology classes; Shannon index of soil types	biotope diversity; biotope heterogeneity; environmental diversity; environmental heterogeneity; environmental variability; environmental variation; geological diversity; habitat diversity; habitat heterogeneity; landscape variation	[6, 8, 12–14, 76, 106–108]

Table A.2 continued

Subject area	Measure category	Measures	Measure variants	Terms	References
soil	soil variables	CV of soil moisture; CV of soil organic matter; CV of soil pH; SD of soil cation concentration; SD of soil pH; soil compaction; soil moisture; soil strength diversity	CV of soil moisture; CV of soil organic matter; CV of soil pH; SD of soil Ca concentration; SD of soil K concentration; SD of soil Mg concentration; SD of soil pH; soil compaction (average measure of soil hardness); soil moisture (scores between 0 and 3); soil strength diversity (based on classes)	environmental complexity; habitat complexity; habitat heterogeneity; resource heterogeneity; soil heterogeneity; spatial variability; structural complexity	[11, 24, 104, 109–112]
soil	termite mounds	number of termite mounds	number of termite mounds	structural complexity	[24]
topography	elevation classes or gradient	CV of elevation; elevation range; elevation range as a percentage of the mean; evenness of elevation classes; maximum elevation; number of mountain peaks; SD of elevation; Shannon index of elevation classes; topographic diversity index	CV of elevation; elevation range; elevation range as a percentage of the mean; evenness of elevation classes; maximum elevation; number of mountain peaks; SD of elevations; Shannon index of elevation classes; topographic diversity index	altitude; altitudinal variation; ecological diversity; elevation; elevational variability; environmental diversity; environmental heterogeneity; environmental variability; environmental variation; habitat complexity; habitat diversity; habitat heterogeneity; landscape heterogeneity; spatial heterogeneity; topographic complexity; topographic diversity; topographic heterogeneity; topographic relief; topographic roughness; topographic variability; topographic variation; topography; variation	[5–9, 13–14, 45, 47, 49, 59–60, 62, 73, 77, 79, 88–90, 95–96, 98, 101, 104, 106–107, 113–154]
topography	microtopographic elements	complexity index of caves; mean distance to stream or river; number of microtopographic elements; percentage of cover of rocks	complexity index of caves; mean distance to stream or river; number of microtopographic elements; percentage of cover of rocks	environmental heterogeneity; habitat complexity; habitat diversity; microhabitat diversity; spatial heterogeneity; topographic heterogeneity	[4, 26, 67, 78, 155]
topography	topographic profile, slope or aspect	average topographic exposure; CV of slopes weighted by area; eastness; SD of potential annual solar radiation (includes aspect variability); SD of profile curvature; slope; topographical complexity scores (classes of 1–5)	average topographic exposure; CV of slopes weighted by area; eastness; SD of potential annual solar radiation (includes aspect variability); SD of profile curvature; slope; topographical complexity scores (classes of 1–5)	environmental heterogeneity; spatial heterogeneity; topographic complexity; topographic heterogeneity; topographic roughness; topographic variability; topographic variation	[23, 26, 67, 130, 139, 149, 156]
vegetation	composite measure	scores of tree species and land cover types; total of scores of five vegetation complexity measures	scores of tree species and land cover types; total of scores of five vegetation complexity measures	environmental heterogeneity; environmental variation; habitat complexity; habitat diversity	[132, 150, 157]
vegetation	cover of vegetation layer (stand structural attribute)	CV of crown diameter; CV of percentage of cover of a vegetation layer; mean percentage vertical cover of canopy layer; mean percentage vertical cover of herb layer; mean percentage vertical cover of shrub layer; percentage of canopy cover; percentage of ground vegetation cover; percentage of shade; percentage of shrub cover; scores of percentage and height of grasses; scores of percentage of cover of canopy layer; scores of percentage of cover of shrub layer; SD of canopy cover; vegetation cover (percentage of points)	CV of crown diameter; CV of herb cover; CV of shrub cover; ground flora (percentage of and height of grasses); mean percentage of vertical cover of field layer (herb layer < 2 m) vegetation; mean percentage of vertical cover of lower canopy layer (5–15 m) vegetation; mean percentage of vertical cover of shrub layer vegetation; mean percentage of vertical cover of upper canopy layer (15–25 m) vegetation; percentage of canopy cover; percentage of ground vegetation cover; percentage of shade at ground level; percentage of shrub cover; SD of canopy cover; shrub canopy cover (per cent as scores between 0 and 3); sub-shrub canopy cover (per cent as scores between 0 and 3); tree canopy cover (per cent as scores between 0 and 3); vegetation cover (percentage of points)	forest structure; habitat complexity; habitat structure; landscape heterogeneity; stand structure; structural complexity; structural diversity; structural heterogeneity; vegetation complexity; vegetation diversity; vegetation structure; vertical structure	[110–111, 157–166]
vegetation	deadwood (stand structural attribute)	inverse of the mean distance to the nearest log; number of types of dead tree parts; percentage of basal area standing dead; percentage of cover of litter; scores of percentage of cover of litter	leaf litter cover (per cent as scores between 0 and 3); log density (inverse distance); number of types of dead tree parts; percentage of basal area standing dead; percentage of leaf litter cover	habitat complexity; habitat diversity; vegetation structure	[110, 157, 167–168]
vegetation	foliage (stand structural attribute)	complexity: sum of horizontal and vertical diversity; foliage height diversity; horizontal diversity; horizontal foliage density; mean number of leaves above a point; number of vegetation layers; vegetation strata index; vertical diversity; vertical foliage diversity	bush horizontal diversity; complexity: sum of horizontal and vertical diversity; foliage height diversity (distribution of foliage between a number of layers); foliage height diversity (of foliage density); foliage height diversity (of vegetation presence); horizontal diversity; horizontal foliage density; mean number of leaves above a point; number of vegetation layers; vegetation strata index (corrected); vegetation strata index (uncorrected); vertical diversity; vertical foliage diversity	environmental complexity; environmental structure; foliage characteristics; habitat complexity; habitat heterogeneity; habitat structure; structural complexity; vegetation complexity; vegetation structure	[112, 146, 155, 158, 161, 169–176]

Table A.2 continued

Subject area	Measure category	Measures	Measure variants	Terms	References
vegetation	plant size and biomass	basal area of plants; collective heterogeneity of resource states; CV of plant height; CV of trunk perimeter; maximum canopy height; number of tree diameter classes; patchiness of tree species distribution; Shannon index of plant diameter classes; Shannon index of plant height classes; Shannon index of plant volume classes	basal area of plants; collective heterogeneity of resource states; CV of tree height; CV of plant height; CV of trunk perimeter; maximum canopy height; number of tree size-classes (DBH); patchiness of tree species distribution (basal area irrespective of species); plant volume diversity; Shannon index applied to pseudo-species (basal area per species and diameter class); Shannon index of DBH classes of trees; Shannon index of perennial plant height diversity; Shannon index of perennial plant species (plant volume)	characteristics of the vegetation; forest structure; habitat diversity; habitat heterogeneity; resource heterogeneity; spatial heterogeneity; spatial variability; storey heterogeneity; structural characteristics; structural diversity; structural heterogeneity; vegetation structure; vegetational physiognomy; vertical structure	[11, 25, 80, 120, 164, 174, 177–182]
vegetation	plant spacing (stand structural attribute)	CV of distance to the nearest tree; density of plants; number of trees; percentage of trees with epiphytes	CV of distance to the nearest tree; density of bird-dispersed plants; density of lianas; density of low trees and shrubs; density of shrubs; density of trees and shrubs; density of zoochoric plants; number of trees >10 cm DBH; number of trees >10 m height; number of trees >20 m height; percentage of trees (> 35 m) with epiphytes; percentage of trees (13–35 m) with epiphytes; percentage of trees (5–13 m) with epiphytes	characteristics of the vegetation; foliage structure; forest structure; habitat complexity; structural characteristics; structural heterogeneity; vegetation structure	[25, 157, 164, 167, 174]
vegetation	species diversity	inverse Simpson index for shrub species diversity; number of food plant species; number of insect species; number of non-woody plant species; number of plant species; number of plant species in flower; number of species needed for 50% basal area; number of woody plant species; ordination of herb layer composition; per cent dissimilarity of woody species; Shannon index of field layer vegetation; Shannon index of tree species	CA1: first axis of correspondence analysis of field layer composition (herbs); CA2: second axis of correspondence analysis of field layer composition (herbs); inverse Simpson index for shrub species diversity; number of anemochoric species; number of bird-dispersed species; number of caterpillar food plant species; number of coniferous tree species; number of fern species; number of *Ficus* species; number of fleshy-fruited plant species; number of flowering plant species; number of food plant species of monophagous butterflies; number of forb species; number of grass tree (*Xanthorrhoea*) species; number of hardwood tree species; number of herb species; number of indigenous insect species; number of Leguminosae species; number of liana species; number of non-fleshy-fruited plant species; number of paperbark (*Melaleuca*) species; number of perennial plant species; number of plant species; number of plant species in flower; number of shrub species; number of species needed for 50% basal area; number of tree and shrub species; number of tree species; number of tree species in general area; number of vascular plant species; number of woody plant species; number of zoochoric plant species; per cent dissimilarity of woody species; Shannon index of field layer vegetation (herb < 2 m); Shannon index of tree species	characteristics of the vegetation; environmental diversity; environmental heterogeneity; floristic characteristics; floristic composition; floristic diversity; floristics; habitat diversity; habitat heterogeneity; insect species richness; landscape heterogeneity; plant diversity; plant richness; resource heterogeneity; spatial heterogeneity; stand structure; structural complexity; taxonomic diversity; tree heterogeneity; vegetation diversity; vertical structure	[20, 24–26, 32–33, 40, 59–61, 75, 118, 120, 122, 127–128, 144–145, 149–150, 153, 159, 161, 174, 177–178, 182–191]
vegetation	stand structural complexity	canopy complexity; CV of pixel values of spectral data; habitat complexity score; mean of MDS scores of vegetation variables (1st axis); mean of the factor scores from the first PCA axis of vegetation variables; median score of vegetation complexity; number of vegetational life-form and density classes; PC2 (principal component 2): shrub density and total basal area; SD of MDS scores of vegetation variables (1st axis); SD of the mean factor score for the first PCA axis of vegetation variables	canopy complexity; CV of pixel values of green spectral band; CV of pixel values of near-infrared spectral band; CV of pixel values of red spectral band; habitat complexity score; mean of MDS scores of vegetation variables (1st axis); mean of the factor scores from the first PCA axis of vegetation variables; median score of vegetation complexity (classes of 0–5); number of vegetational life-form and density classes; PC2: principal component 2: shrub density and total basal area; SD of MDS scores of vegetation variables (1st axis); SD of the mean factor score for the first PCA axis of vegetation variables	habitat complexity; habitat diversity; habitat heterogeneity; habitat structure; landscape diversity; patchiness; spatial heterogeneity; structural heterogeneity; vegetation complexity; vegetation heterogeneity; vegetation structure; vertical complexity	[61, 143, 157, 160, 169, 188, 192–194]

A.4 Additional figures

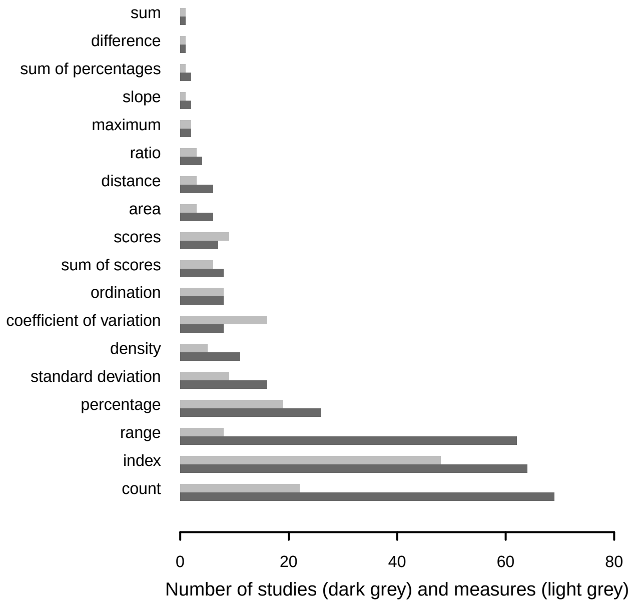

Figure A.1 Calculation methods applied in the quantification of EH, ordered according to the frequency of studies using each method (dark-grey bars). Light-grey bars represent the number of measures computed through each method.

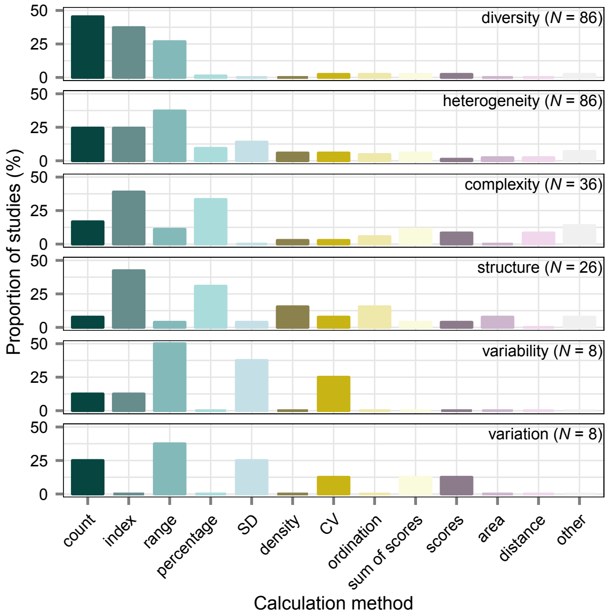

Figure A.2 Proportion of studies using each calculation method in combination with a particular noun for terms for EH. Only the most common nouns are displayed in the order of their frequency. The noun "richness" (*N* = 10) only occurred in combination with count measures and was omitted for clarity. The 100% reference level for each panel is *N*, the total number of studies using each noun, respectively. Calculation methods: SD, standard deviation; CV, coefficient of variation; "other" combines various rare calculation methods.

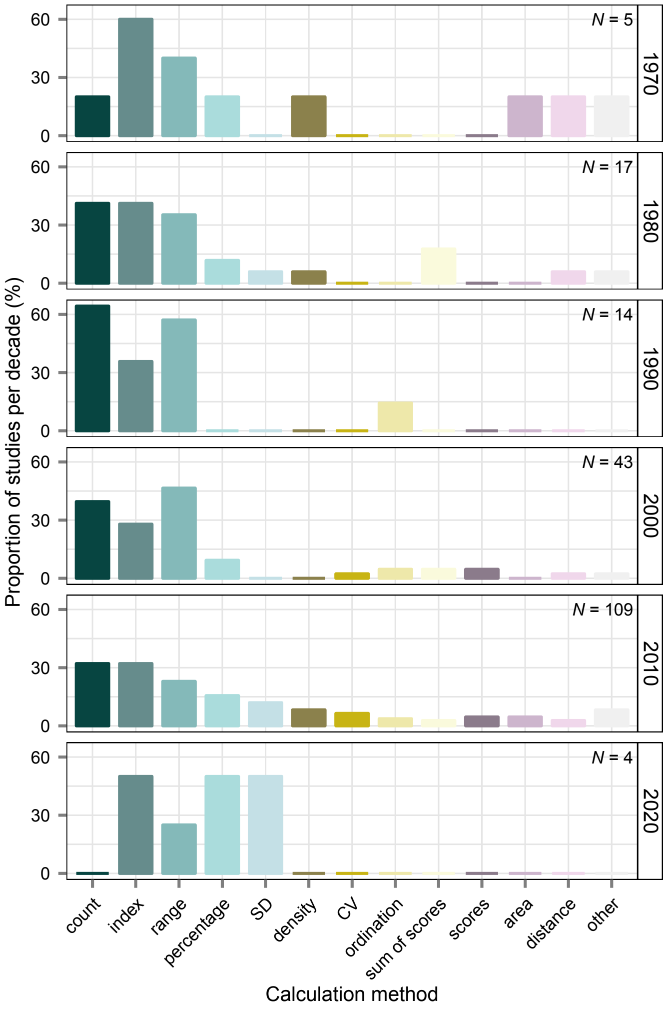

Figure A.3 Proportion of studies using each calculation method per decade. The 100% reference level for each panel is *N*, the total number of studies per decade. Calculation methods: SD, standard deviation; CV, coefficient of variation; "other" combines various rare calculation methods.

B
Supporting information to chapter 3

B.1 Literature search in *Web of Science*

Our advanced search in *Web of Science* covered all languages and document types until 19th of April 2011. We used the *topic* field, which searches titles, abstracts, author keywords, and "Keywords Plus". The latter are derived by Thomson Reuters from frequent words in the titles of the references cited by an article. Although this approach led to many irrelevant results, we believe that insufficiencies in our search string should have been buffered by the comprehensiveness of this search type.

The search terms were as follows (split into two separate searches due to a restriction in the number of terms per search by Web of Science):

> ts=("habitat heterogeneity" OR "habitat diversity" OR "habitat complexity" OR "habitat number" OR "biotop$$ heterogeneity" OR "biotop$$ diversity" OR "biotop$$ complexity" OR "biotop$$ number" OR "ecotop$$ heterogeneity" OR "ecotop$$ diversity" OR "ecotop$$ complexity" OR "ecotop$$ number" OR "biom$$ heterogeneity" OR "biom$$ diversity" OR "biom$$ complexity" OR "biom$$ number" OR "structural heterogeneity" OR "structural diversity" OR "structural complexity" OR "spatial heterogeneity" OR "spatial complexity" OR "topograph* heterogeneity" OR "topograph* diversity" OR "topograph* complexity" OR "relief heterogeneity" OR "relief diversity" OR "relief complexity" OR "aspect heterogeneity" OR "aspect diversity" OR "aspect complexity" OR "architectur$$ heterogeneity" OR "architectur$$ diversity" OR "architectur$$ complexity" OR "land use heterogeneity" OR "land use diversity" OR "land use complexity" OR "altitud* heterogeneity" OR "altitud* complexity" OR "elevation$$ heterogeneity" OR "elevation$$ complexity" OR "environment$$ heterogeneity" OR "environment$$ diversity" OR "environment$$ complexity" OR "climat$$ heterogeneity" OR "climat$$ diversity" OR "climat$$ complexity" OR "soil heterogeneity" OR "soil complexity" OR "foliage heterogeneity" OR "foliage diversity" OR "foliage complexity" OR "foliage height heterogeneity" OR "foliage height diversity" OR "foliage height complexity" OR "vegetation$$ heterogeneity" OR "vegetation$$ diversity" OR "vegetation$$ complexity" OR "NDVI" OR "normalized difference vegetation index" OR "geoheterogeneity" OR "geodiversity" OR "geocomplexity" OR "geograph* heterogeneity" OR "geograph* diversity" OR "geograph* complexity" OR "landscape heterogeneity" OR "landscape diversity" OR "landscape complexity") AND ts=("species diversity" OR "species richness" OR "species number" OR "species density").

We deliberately included "species" only instead of further defining taxonomic groups, such as "mammal" or "plant diversity", to avoid a taxonomic bias in our search. We detected more than 2,600 articles, which were further restricted by exclusion of particular subject areas and additional keywords:

> Refined by: [excluding] Subject Areas=(MARINE & FRESHWATER BIOLOGY OR WATER RESOURCES OR OCEANOGRAPHY OR MICROBIOLOGY OR PALEONTOLOGY OR MYCOLOGY OR FISHERIES OR BIOCHEMISTRY & MOLECULAR BIOLOGY OR BIOTECHNOLOGY & APPLIED MICROBIOLOGY OR LIMNOLOGY); NOT ts=(fish* OR marine OR aquatic OR macrobenthos OR macrobenthic OR benthic OR benthos OR pelagic OR pelago OR diatom* OR plankton* OR zooplankton* OR phytoplankton* OR nekton* OR coral$ OR "coral reef$" OR "deep sea" OR seafloor OR "sea floor" OR bivalv* OR alga OR algae OR mussel$ OR bacteri* OR virus* OR viral OR archaea* OR microbe* OR microbiol* OR microbial* OR mycolog* OR fungus OR fungi OR fungal).

Finally, we checked the titles, abstracts and often the full articles of 1,732 studies to determine if they were relevant and met our inclusion criteria.

B.2 Results from sensitivity analyses: variation of within-study correlation ρ

In our meta-analysis, we estimated the between-study variance component τ^2 assuming a value of 0.8 for the within-study correlation ρ, i.e. the mean correlation between all effect size estimates per study. Sensitivity analyses varying ρ between 0 and 1 in increments of 0.1 indicate that values of τ^2, point estimates *b* and standard errors *SE* were robust to our choice of ρ for any of the data subsets.

Table B.1 Sensitivity analysis on ρ: complete dataset.

ρ	b	SE	τ^2
0.0	0.62861	0.03403	0.148057
0.1	0.62861	0.03403	0.148059
0.2	0.62861	0.03403	0.148062
0.3	0.62861	0.03403	0.148064
0.4	0.62861	0.03403	0.148066
0.5	0.62861	0.03403	0.148068
0.6	0.62861	0.03403	0.148071
0.7	0.62861	0.03403	0.148073
0.8	0.62861	0.03403	0.148075
0.9	0.62861	0.03403	0.148077
1.0	0.62861	0.03403	0.148079

Table B.2 Sensitivity analysis on ρ: equal-area studies.

ρ	b	SE	τ^2
0.0	0.4708	0.04658	0.133189
0.1	0.4708	0.04658	0.133192
0.2	0.4708	0.04658	0.133195
0.3	0.4708	0.04658	0.133199
0.4	0.4708	0.04658	0.133202
0.5	0.4708	0.04658	0.133205
0.6	0.4708	0.04658	0.133208
0.7	0.4708	0.04658	0.133212
0.8	0.4708	0.04658	0.133215
0.9	0.4708	0.04658	0.133218
1.0	0.4708	0.04658	0.133221

Table B.3 Sensitivity analysis on ρ: subgroup I.

ρ	b	SE	τ^2
0.0	0.61182	0.04102	0.132844
0.1	0.61182	0.04102	0.132846
0.2	0.61183	0.04102	0.132848
0.3	0.61183	0.04102	0.132851
0.4	0.61183	0.04102	0.132853
0.5	0.61183	0.04102	0.132856
0.6	0.61183	0.04102	0.132858
0.7	0.61183	0.04102	0.132860
0.8	0.61183	0.04102	0.132863
0.9	0.61183	0.04102	0.132865
1.0	0.61183	0.04102	0.132867

Table B.4 Sensitivity analysis on ρ: subgroup II.

ρ	b	SE	τ^2
0.0	0.8002	0.07106	0.192370
0.1	0.8002	0.07106	0.192389
0.2	0.8002	0.07106	0.192408
0.3	0.8002	0.07106	0.192427
0.4	0.8002	0.07106	0.192446
0.5	0.8002	0.07106	0.192465
0.6	0.8002	0.07106	0.192484
0.7	0.8002	0.07106	0.192503
0.8	0.8002	0.07106	0.192521
0.9	0.8002	0.07106	0.192540
1.0	0.8002	0.07106	0.192559

Table B.5 Sensitivity analysis on ρ: subgroup III.

ρ	b	SE	τ^2
0.0	0.6302	0.07761	0.262555
0.1	0.6302	0.07761	0.262567
0.2	0.6302	0.07761	0.262580
0.3	0.6302	0.07761	0.262593
0.4	0.6302	0.07761	0.262605
0.5	0.6302	0.07761	0.262618
0.6	0.6302	0.07761	0.262630
0.7	0.6302	0.07761	0.262643
0.8	0.6302	0.07761	0.262656
0.9	0.6302	0.07761	0.262668
1.0	0.6302	0.07761	0.262681

B.3 Collinearity of covariates

Table B.6 Correlation tests for study characteristics of subgroup I (EH measure categories elevation and land cover diversity). Values are Pearson product-moment correlations between continuous variables, polyserial correlations between continuous and categorical variables, and polychoric correlations between categorical variables (R package *polycor*; Fox, J. (2010). polycor: Polychoric and Polyserial Correlations. R package version 0.7-8. http://CRAN.R-project.org/package=polycor). Only covariates with a correlation of less than |0.6| were combined in a model. For details on covariates see Table 3.2 (EH = EH measure category).

	equal area	grain	extent	EH	PET	habitat	island	broad taxon	fine taxon
equal area	1.00								
grain	0.10	1.00							
extent	-0.32	0.37	1.00						
EH	-0.36	0.38	0.55	1.00					
PET	-0.25	-0.00	0.37	0.19	1.00				
habitat	0.10	-0.36	-0.27	-0.23	-0.10	1.00			
island	-0.71	0.10	-0.05	0.20	-0.21	-0.19	1.00		
broad taxon	-0.10	0.21	0.39	0.04	0.30	-0.19	-0.28	1.00	
fine taxon	0.37	0.19	-0.16	-0.09	-0.29	-0.25	-0.09	-0.60	1.00

Table B.7 Correlation tests for study characteristics of subgroup II (EH measure categories vegetation complexity and plant diversity). Values are Pearson product-moment correlations between continuous variables, polyserial correlations between continuous and categorical variables, and polychoric correlations between categorical variables (R package *polycor*). Only covariates with a correlation of less than |0.6| were combined in a model. For details on covariates see Table 3.2 (EH = EH measure category).

	equal area	grain	extent	EH	PET	habitat	island	broad taxon	fine taxon
equal area	1.00								
grain	-0.32	1.00							
extent	-0.26	0.51	1.00						
EH	0.19	-0.48	-0.41	1.00					
PET	0.09	0.17	-0.11	-0.09	1.00				
habitat	-0.08	-0.05	0.33	-0.10	-0.39	1.00			
island	0.18	-0.11	0.36	-0.17	-0.75	0.57	1.00		
broad taxon	-0.25	0.52	0.17	-0.06	0.66	-0.49	-0.72	1.00	
fine taxon	0.03	-0.40	-0.25	0.37	-0.22	0.22	0.17	-0.36	1.00

B.4 References to studies included in the meta-analysis

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B.5 Data included in the meta-analysis

Table B.8 Summary of data used in the meta-analysis. ref: study references according to numbering in Section B.4; realm: Afr: Afrotropic, Aus: Australasia, Ind: Indo-Malay, Nea: Nearctic, Neo: Neotropic, Oce: Oceania, Pal: Palearctic, mix: mixed; biome: 1: boreal forests/ taiga, 2: deserts and xeric shrublands, 3: Mediterranean forests, woodlands, and scrub, 4: montane grasslands and shrublands, 5: temperate broadleaf and mixed forests, 6: temperate coniferous forests, 7: temperate grasslands, savannas, and shrublands, 8: tropical and subtropical dry broadleaf forests, 9: tropical and subtropical grasslands, savannas, and shrublands, 10: tropical and subtropical moist broadleaf forests, 11: tundra, 12: mixed; habitat – main habitat type: agr: agricultural, for: forest, gra: grassland, mon: montane, xer: xeric, mix: mixed; PET – mean PET (mm/a); taxon: pla: plants, inv: invertebrates, bir: birds, her: herptiles, mam: mammals, mix: mixed vertebrates; growth – growth form: ani: animal, her: herbs, shr: shrubs or trees, mix: mixed plants; thermo – thermoregulation: ect: ectotherm, end: endotherm, mix: mixed, pla: plant; trophic – trophic group: aut: autotroph, car: carnivore, det: detritivore, fru: frugivore, her: herbivore, ins: insectivore, omn: omnivore, mix: mixed; EH – EH subject area: lan: land cover, veg: vegetation, cli: climate, soi: soil, top: topography, mix: mixed; EHcat – EH measure category: lcd: land cover diversity, lcp: land cover proportion, pat: patchiness, pla: plant diversity, vec: vegetation complexity, ved: vegetation dimension, cli: climate, sod: soil diversity, sov: soil variables, ele: elevation diversity, mic: microtopography, pro: profile, mix: mixed; unit – unit of analysis: gri: grid cell, isl: island, plo: plot, pol: polygon, tra: transect; EA – equal area; grain – spatial grain class: 1: $\leq 0.01\ \mathrm{km}^2$, 2: $> 0.01\ \mathrm{km}^2 - 1\ \mathrm{km}^2$, 3: $> 1\ \mathrm{km}^2 - 100\ \mathrm{km}^2$, 4: $> 100\ \mathrm{km}^2$; extent – spatial extent class: 1: $\leq 1{,}000\ \mathrm{km}^2$, 2: $> 1{,}000\ \mathrm{km}^2 - 10{,}000\ \mathrm{km}^2$, 3: $> 10{,}000\ \mathrm{km}^2 - 1{,}000{,}000\ \mathrm{km}^2$, 4: $> 1{,}000{,}000\ \mathrm{km}^2$; n – sample size; ES – effect size estimate (Fisher's *z*); var – variance. Categories for island, tropical, and equal area mean "no" (0) and "yes" (1).

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EHcat	unit	EA	grain	extent	n	ES	var
1	Neo	12	mix	1	1	1556.33	pla	her	pla	aut	top	ele	isl	0	4	4	31	1.10	0.04
1	Neo	12	mix	1	1	1556.33	pla	her	pla	aut	top	ele	isl	0	4	4	16	-0.08	0.08
1	Neo	12	mix	1	1	1556.33	pla	her	pla	aut	top	ele	isl	0	4	4	21	0.60	0.06
1	Neo	12	mix	1	1	1556.33	pla	her	pla	aut	top	ele	isl	0	4	4	10	1.42	0.14
1	Neo	12	mix	1	1	1556.33	pla	her	pla	aut	top	ele	isl	0	4	4	9	1.12	0.17
2	Pal	12	mix	0	0	706.53	pla	shr	pla	aut	top	ele	gri	0	4	4	168	0.67	0.01
2	Pal	12	mix	0	0	622.11	pla	shr	pla	aut	top	ele	gri	0	4	4	108	0.24	0.01
3	mix	12	mix	1	1	1614.33	bir	ani	end	mix	top	ele	isl	0	4	4	14	1.50	0.09
4	Afr	12	mix	0	1	1817.80	pla	her	pla	aut	top	ele	pol	0	4	4	29	0.56	0.04
5	Afr	9	gra	0	1	1587.66	pla	mix	pla	aut	top	ele	plo	1	1	3	102	0.45	0.01
5	Afr	9	gra	0	1	1587.66	pla	mix	pla	aut	top	ele	plo	1	1	3	102	0.31	0.01
5	Afr	9	gra	0	1	1587.66	pla	mix	pla	aut	top	ele	plo	1	1	3	102	0.32	0.01
5	Afr	9	gra	0	1	1587.66	pla	mix	pla	aut	top	ele	plo	1	1	3	102	0.16	0.01
6	Afr	12	mix	0	0	1664.09	mam	ani	end	mix	veg	pla	gri	1	4	4	111	1.31	0.01
6	Afr	12	mix	0	0	1664.09	pla	shr	pla	aut	top	ele	gri	1	4	4	65	0.66	0.02
7	Pal	3	mix	0	0	1074.51	bir	ani	end	mix	lan	lcd	gri	1	3	2	106	1.33	0.01
7	Pal	3	mix	0	0	1074.51	her	ani	ect	mix	lan	lcd	gri	1	3	2	106	0.73	0.01
7	Pal	3	mix	0	0	1074.51	her	ani	ect	mix	lan	lcd	gri	1	3	2	106	0.74	0.01
7	Pal	3	mix	0	0	1074.51	inv	ani	ect	her	lan	lcd	gri	1	3	2	106	1.07	0.01
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	1.59	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	2.09	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	car	veg	vec	plo	1	2	1	5	1.59	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	car	veg	vec	plo	1	2	1	5	2.09	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	ins	veg	vec	plo	1	2	1	5	1.33	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	ins	veg	vec	plo	1	2	1	5	1.83	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	fru	veg	vec	plo	1	2	1	5	1.59	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	fru	veg	vec	plo	1	2	1	5	2.09	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	1.59	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	1.42	0.50

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	1.59	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	2.09	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	1.59	0.50
8	Neo	9	for	0	1	1753.37	mam	ani	end	mix	veg	vec	plo	1	2	1	5	1.42	0.50
9	Pal	5	mix	0	0	908.56	inv	ani	ect	mix	lan	lcd	pol	0	3	2	16	1.44	0.08
10	Pal	5	for	0	0	965.68	bir	ani	end	mix	lan	lcd	plo	0	2	1	27	0.53	0.04
10	Pal	5	for	0	0	965.68	inv	ani	ect	car	lan	lcd	plo	0	2	1	27	-0.04	0.04
10	Pal	5	for	0	0	965.68	inv	ani	ect	car	lan	lcd	plo	0	2	1	27	0.13	0.04
10	Pal	5	for	0	0	965.68	bir	ani	end	mix	lan	lcp	plo	0	2	1	27	-0.63	0.04
10	Pal	5	for	0	0	965.68	inv	ani	ect	car	lan	lcp	plo	0	2	1	27	-0.08	0.04
10	Pal	5	for	0	0	965.68	inv	ani	ect	car	lan	lcp	plo	0	2	1	27	0.25	0.04
11	Pal	5	gra	0	0	911.03	inv	ani	ect	car	lan	lcp	pol	1	2	2	42	0.23	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	her	lan	lcp	pol	1	2	2	42	0.35	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	her	lan	lcp	pol	1	2	2	42	0.43	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	car	lan	lcp	pol	1	2	2	42	0.09	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	her	lan	lcp	pol	1	2	2	42	0.32	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	her	lan	lcp	pol	1	2	2	42	0.38	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	car	lan	lcp	pol	1	2	2	42	0.33	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	her	lan	lcp	pol	1	2	2	42	0.48	0.03
11	Pal	5	gra	0	0	911.03	inv	ani	ect	her	lan	lcp	pol	1	2	2	42	0.53	0.03
12	Pal	3	for	0	0	1030.34	inv	ani	ect	her	veg	vec	pol	0	3	2	13	-0.13	0.10
12	Pal	3	for	0	0	1030.34	inv	ani	ect	her	veg	vec	pol	0	3	2	13	-0.34	0.10
12	Pal	3	for	0	0	1030.34	inv	ani	ect	her	veg	vec	pol	0	3	2	13	-0.02	0.10
12	Pal	3	for	0	0	1030.34	inv	ani	ect	her	veg	vec	pol	0	3	2	13	-0.15	0.10
12	Pal	3	for	0	0	1030.34	inv	ani	ect	her	veg	vec	pol	0	3	2	13	-0.27	0.10
13	Neo	12	mix	0	0	1297.74	bir	ani	end	car	veg	vec	gri	1	4	4	245	1.24	0.00
14	Pal	3	agr	0	0	1344.64	bir	ani	end	mix	lan	lcd	gri	1	1	1	32	0.47	0.03
14	Pal	3	agr	0	0	1344.64	bir	ani	end	mix	lan	lcd	gri	1	1	1	40	0.30	0.03
14	Pal	3	agr	0	0	1344.64	bir	ani	end	mix	lan	lcd	gri	1	1	1	25	0.60	0.05
15	Nea	5	agr	0	0	1100.30	bir	ani	end	mix	veg	pla	pol	1	2	1	6	0.13	0.33
16	Nea	7	for	0	0	1088.63	bir	ani	end	mix	veg	vec	pol	0	3	2	12	1.14	0.11
17	Pal	5	mix	1	0	591.80	inv	ani	ect	omn	veg	pla	isl	0	3	3	17	1.29	0.07
17	Pal	5	mix	1	0	591.80	inv	ani	ect	omn	lan	lcd	isl	0	3	3	18	1.63	0.07
17	Pal	5	mix	1	0	591.80	inv	ani	ect	omn	lan	lcd	isl	0	3	3	18	1.54	0.07
18	Aus	12	mix	0	1	1923.13	pla	shr	pla	aut	lan	lcd	gri	0	4	3	15	0.08	0.08
18	Aus	12	mix	0	1	1923.13	pla	shr	pla	aut	lan	lcd	gri	0	4	3	15	0.12	0.08
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	mix	mix	pol	0	3	4	21	0.79	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	soi	sod	pol	0	3	4	21	0.62	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	lan	lcd	pol	0	3	4	21	0.66	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	top	ele	pol	0	3	4	21	0.52	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	mix	mix	pol	0	3	4	21	0.50	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	lan	lcd	pol	0	3	4	21	0.45	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	mix	mix	pol	0	3	4	21	0.48	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	lan	lcd	pol	0	3	4	21	0.65	0.06

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	top	ele	pol	0	3	4	21	0.78	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	mix	mix	pol	0	3	4	21	0.48	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	lan	lcd	pol	0	3	4	21	0.56	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	mix	mix	pol	0	3	4	21	0.81	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	soi	sod	pol	0	3	4	21	0.74	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	lan	lcd	pol	0	3	4	21	0.46	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	top	ele	pol	0	3	4	21	0.56	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	mix	mix	pol	0	3	4	21	0.62	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	soi	sod	pol	0	3	4	21	0.54	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	lan	lcd	pol	0	3	4	21	0.65	0.06
19	Neo	12	for	0	1	1649.82	inv	ani	ect	her	top	ele	pol	0	3	4	21	0.42	0.06
20	Neo	10	mix	0	1	1624.05	mam	ani	end	mix	top	mic	plo	0	1	1	20	0.03	0.06
20	Neo	10	mix	0	1	1624.05	mam	ani	end	mix	cli	cli	plo	0	1	1	7	1.41	0.25
20	Neo	10	mix	0	1	1624.05	mam	ani	end	mix	cli	cli	plo	0	1	1	7	0.58	0.25
20	Neo	10	mix	0	1	1624.05	mam	ani	end	mix	cli	cli	plo	0	1	1	7	1.01	0.25
21	Nea	2	xer	1	0	1764.03	her	ani	ect	mix	top	ele	isl	0	4	3	25	0.61	0.05
21	Nea	2	xer	1	0	1764.03	her	ani	ect	mix	veg	pla	isl	0	4	3	25	1.14	0.05
21	Nea	2	xer	1	0	1764.03	her	ani	ect	mix	veg	ved	isl	0	4	3	12	0.81	0.11
22	Pal	5	mix	0	0	1011.63	inv	ani	ect	her	top	ele	gri	0	4	3	43	0.51	0.02
23	mix	12	mix	1	0	913.45	pla	mix	pla	aut	top	ele	isl	0	4	4	25	0.41	0.05
23	mix	12	mix	1	0	913.45	pla	mix	pla	aut	top	ele	isl	0	4	4	25	0.64	0.05
23	mix	12	mix	1	0	913.45	inv	ani	ect	mix	top	ele	isl	0	4	4	25	0.03	0.05
23	mix	12	mix	1	0	913.45	inv	ani	ect	mix	top	ele	isl	0	4	4	25	0.46	0.05
23	mix	12	mix	1	0	913.45	bir	ani	end	mix	top	ele	isl	0	4	4	25	0.07	0.05
23	mix	12	mix	1	0	913.45	bir	ani	end	mix	top	ele	isl	0	4	4	25	0.10	0.05
23	mix	12	mix	1	0	913.45	mam	ani	end	mix	top	ele	isl	0	4	4	25	0.47	0.05
23	mix	12	mix	1	0	913.45	inv	ani	ect	mix	veg	pla	isl	0	4	4	25	1.06	0.05
23	mix	12	mix	1	0	913.45	inv	ani	ect	mix	veg	pla	isl	0	4	4	25	0.87	0.05
23	mix	12	mix	1	0	913.45	bir	ani	end	mix	veg	pla	isl	0	4	4	25	0.83	0.05
23	mix	12	mix	1	0	913.45	bir	ani	end	mix	veg	pla	isl	0	4	4	25	0.75	0.05
23	mix	12	mix	1	0	913.45	mam	ani	end	mix	veg	pla	isl	0	4	4	25	0.65	0.05
23	mix	12	mix	1	0	913.45	bir	ani	end	mix	veg	pla	isl	0	4	4	25	0.96	0.05
23	mix	12	mix	1	0	913.45	bir	ani	end	mix	veg	pla	isl	0	4	4	25	0.95	0.05
24	Pal	5	agr	0	0	698.39	inv	ani	ect	car	lan	lcp	pol	1	2	3	21	0.65	0.06
25	Aus	3	for	0	0	1386.44	bir	ani	end	mix	veg	vec	plo	1	2	1	48	0.11	0.02
25	Aus	3	for	0	0	1386.44	bir	ani	end	mix	veg	ved	plo	1	2	1	48	0.00	0.02
25	Aus	3	for	0	0	1386.44	bir	ani	end	mix	veg	vec	plo	1	2	1	48	0.30	0.02
25	Aus	3	for	0	0	1386.44	bir	ani	end	mix	veg	ved	plo	1	2	1	48	-0.26	0.02
25	Aus	3	for	0	0	1386.44	bir	ani	end	mix	veg	ved	plo	1	2	1	48	0.37	0.02
25	Aus	3	for	0	0	1386.44	bir	ani	end	mix	veg	vec	plo	1	2	1	48	0.21	0.02
26	Oce	12	mix	1	0	1239.35	inv	ani	ect	mix	lan	lcd	isl	0	4	3	14	1.90	0.09
27	Neo	8	for	0	1	1821.47	inv	ani	ect	her	veg	pla	tra	1	1	1	60	1.78	0.02
28	Nea	12	mix	0	0	712.01	pla	shr	pla	aut	cli	cli	gri	0	4	4	337	0.20	0.00
28	Nea	12	mix	0	0	712.01	pla	shr	pla	aut	cli	cli	gri	0	4	4	337	0.44	0.00

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
28	Nea	12	mix	0	0	712.01	bir	ani	end	mix	top	ele	gri	0	4	4	337	0.31	0.00
28	Nea	12	mix	0	0	712.01	bir	ani	end	mix	cli	cli	gri	0	4	4	337	0.44	0.00
28	Nea	12	mix	0	0	712.01	her	ani	ect	mix	cli	cli	gri	0	4	4	337	0.46	0.00
28	Nea	12	mix	0	0	712.01	her	ani	ect	mix	cli	cli	gri	0	4	4	337	0.59	0.00
29	Nea	12	for	0	0	912.38	bir	ani	end	mix	lan	lcd	pol	0	3	3	30	0.80	0.04
30	Nea	12	mix	0	0	562.63	mam	ani	end	her	lan	lcp	pol	0	4	4	12	1.42	0.11
30	Pal	12	mix	0	0	540.03	mam	ani	end	her	lan	lcp	pol	0	4	4	9	0.58	0.17
30	Nea	12	mix	0	0	562.63	mam	ani	end	her	lan	lcd	pol	0	4	4	12	0.37	0.11
30	Pal	12	mix	0	0	540.03	mam	ani	end	her	lan	lcd	pol	0	4	4	9	0.81	0.17
30	Nea	12	mix	0	0	562.63	mam	ani	end	her	veg	pla	pol	0	4	4	12	0.76	0.11
30	Pal	12	mix	0	0	540.03	mam	ani	end	her	veg	pla	pol	0	4	4	9	0.60	0.17
30	Nea	12	mix	0	0	562.63	mam	ani	end	her	veg	pla	pol	0	4	4	12	0.54	0.11
30	Pal	12	mix	0	0	540.03	mam	ani	end	her	veg	pla	pol	0	4	4	9	0.44	0.17
31	Ind	10	for	1	1	1263.64	bir	ani	end	mix	lan	lcd	isl	0	3	3	45	1.25	0.02
31	Ind	10	for	1	1	1263.64	bir	ani	end	mix	lan	lcd	isl	0	3	3	37	0.77	0.03
31	Ind	10	for	1	1	1263.64	bir	ani	end	mix	lan	lcd	isl	0	3	3	7	2.18	0.25
32	Pal	3	mix	1	0	1132.54	inv	ani	ect	her	top	ele	isl	0	4	3	31	0.47	0.04
33	Nea	11	gra	1	0	395.53	pla	mix	pla	aut	lan	lcd	isl	0	2		34	2.18	0.03
33	Nea	11	gra	1	0	395.53	pla	mix	pla	aut	top	ele	isl	0	2		34	1.60	0.03
34	Ind	10	for	1	1	1263.64	inv	ani	ect	her	lan	lcd	isl	0	4	3	23	0.48	0.05
35	mix	12	mix	0	0	790.12	bir	ani	end	mix	top	ele	gri	1	4	4	3433	0.29	0.00
35	mix	12	mix	0	0	790.12	bir	ani	end	mix	top	ele	gri	1	4	4	3088	0.31	0.00
35	mix	12	mix	1	0	790.12	bir	ani	end	mix	top	ele	gri	1	4	4	345	0.05	0.00
36	Neo	10	for	0	1	1623.00	bir	ani	end	ins	cli	cli	pol	1	4	3	100	0.50	0.01
36	Neo	10	for	0	1	1623.00	bir	ani	end	ins	cli	cli	pol	1	4	3	100	0.05	0.01
36	Neo	10	for	0	1	1623.00	bir	ani	end	ins	top	ele	pol	1	4	3	100	0.04	0.01
36	Neo	10	for	0	1	1623.00	bir	ani	end	ins	top	ele	pol	1	4	3	100	0.53	0.01
36	Neo	10	for	0	1	1623.00	bir	ani	end	ins	soi	sod	pol	1	4	3	100	0.39	0.01
37	Pal	12	agr	0	0	829.54	bir	ani	end	mix	lan	lcd	plo	1	1	2	60	0.89	0.02
37	Pal	12	agr	0	0	829.54	bir	ani	end	mix	lan	lcp	plo	1	1	2	60	0.31	0.02
37	Pal	12	agr	0	0	829.54	bir	ani	end	mix	lan	lcd	plo	1	1	2	60	0.14	0.02
37	Pal	12	agr	0	0	829.54	bir	ani	end	mix	lan	lcp	plo	1	1	2	60	0.47	0.02
38	Pal	6	for	0	0	680.47	pla	mix	pla	aut	veg	pla	plo	1	1	1	93	-0.03	0.01
39	Pal	3	for	1	0	1030.72	inv	ani	ect	mix	top	ele	isl	0	4	3	32	0.68	0.03
39	Pal	3	for	1	0	1030.72	inv	ani	ect	mix	lan	lcd	isl	0	4	3	29	0.40	0.04
40	Pal	12	mix	0	0	1050.06	pla	her	pla	aut	top	ele	gri	1	4	3	240	0.81	0.00
40	Pal	12	mix	0	0	1050.06	pla	her	pla	aut	cli	cli	gri	1	4	3	240	0.71	0.00
40	Pal	12	mix	0	0	1050.06	pla	her	pla	aut	cli	cli	gri	1	4	3	240	0.50	0.00
41	Pal	5	agr	1	0	616.09	pla	mix	pla	aut	lan	lcd	plo	1	2	3	309	0.64	0.00
41	Pal	5	agr	1	0	616.09	bir	ani	end	mix	lan	lcd	plo	1	2	3	176	0.18	0.01
41	Pal	5	agr	1	0	616.09	pla	mix	pla	aut	lan	lcd	plo	1	2	3	309	0.43	0.00
41	Pal	5	agr	1	0	616.09	bir	ani	end	mix	lan	lcd	plo	1	2	3	176	0.34	0.01
42	Pal	5	agr	0	0	727.82	mam	ani	end	mix	lan	lcp	pol	1	2	1	11	-0.34	0.12
42	Pal	5	agr	0	0	727.82	mam	ani	end	mix	lan	lcp	pol	1	2	1	11	0.11	0.12

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
42	Pal	5	agr	0	0	727.82	mam	ani	end	mix	lan	lcp	pol	1	2	1	22	-0.05	0.05
43	Pal	12	mix	0	0	717.38	mam	ani	end	mix	top	ele	gri	1	4	4	1570	0.00	0.00
43	Pal	12	mix	0	0	717.38	mam	ani	end	mix	lan	lcd	gri	1	4	4	1570	0.19	0.00
44	Aus	5	for	0	0	1196.38	mam	ani	end	mix	lan	lcd	plo	0	2	1	11	1.82	0.12
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	12	1.09	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	12	1.16	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	12	0.45	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	soi	sod	gri	1	4	3	12	0.61	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	12	0.49	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	12	0.38	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	12	0.97	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	12	0.45	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	12	0.51	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	12	0.39	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	12	0.35	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	12	0.31	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	12	0.39	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	12	0.31	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	12	0.91	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	12	-0.34	0.11
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	24	0.64	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	24	0.64	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	24	0.36	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	soi	sod	gri	1	4	3	24	0.64	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	24	0.27	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	24	0.19	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	24	0.72	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	24	0.66	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	24	0.26	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	24	0.14	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	24	0.30	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	24	0.20	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	24	0.27	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	24	0.08	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	24	0.46	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	24	-0.17	0.05
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	63	0.60	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	63	0.51	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	63	0.60	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	soi	sod	gri	1	4	3	63	0.44	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	63	0.31	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	63	0.34	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	63	0.59	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	63	0.43	0.02

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	63	0.32	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	63	0.25	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	63	0.26	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	63	0.32	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	63	0.23	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	63	0.06	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	63	0.48	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	63	-0.04	0.02
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	252	0.49	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	252	0.51	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	252	0.54	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	soi	sod	gri	1	4	3	252	0.35	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	252	0.20	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	4	3	252	0.26	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	252	0.45	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	4	3	252	0.36	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	252	0.20	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	252	0.15	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	252	0.27	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	252	0.32	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	252	0.16	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	4	3	252	0.06	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	252	0.40	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	4	3	252	-0.23	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	3	3	2420	0.32	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	3	3	2420	0.37	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	3	3	2420	0.40	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	soi	sod	gri	1	3	3	2420	0.28	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	3	3	2420	-0.01	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	top	ele	gri	1	3	3	2420	0.09	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	3	3	2420	0.33	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcd	gri	1	3	3	2420	0.25	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	3	3	2420	-0.01	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	3	3	2420	-0.05	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	3	3	2420	0.12	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	3	3	2420	0.16	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	3	3	2420	-0.02	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	cli	cli	gri	1	3	3	2420	-0.05	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	3	3	2420	0.21	0.00
45	Nea	12	for	0	0	970.10	mix	ani	mix	mix	lan	lcp	gri	1	3	3	2420	-0.18	0.00
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	2	2	18	0.54	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	2	2	18	0.46	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	2	2	18	0.97	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	2	2	18	0.50	0.07

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.62	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.62	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	1.07	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.47	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.56	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.55	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	0.95	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.45	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.56	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.48	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	0.83	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.48	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.60	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.42	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	0.76	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.52	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcp	pol	1	2	2	18	0.63	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcd	pol	1	2	2	18	0.39	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	pat	pol	1	2	2	18	0.68	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	top	pro	pol	1	2	2	18	0.05	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcp	pol	1	3	2	18	0.47	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcd	pol	1	3	2	18	0.33	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	pat	pol	1	3	2	18	0.65	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	top	pro	pol	1	3	2	18	0.09	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcp	pol	1	3	2	18	0.37	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcd	pol	1	3	2	18	0.26	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	pat	pol	1	3	2	18	0.55	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	top	pro	pol	1	3	2	18	0.14	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcp	pol	1	3	2	18	0.34	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcd	pol	1	3	2	18	0.27	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	pat	pol	1	3	2	18	0.48	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	top	pro	pol	1	3	2	18	0.24	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcp	pol	1	3	2	18	0.38	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	lcd	pol	1	3	2	18	0.28	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	lan	pat	pol	1	3	2	18	0.48	0.07
46	Pal	5	agr	0	0	725.42	pla	mix	pla	aut	top	pro	pol	1	3	2	18	0.35	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	2	2	18	0.39	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	2	2	18	0.40	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	2	2	18	0.81	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	2	2	18	0.60	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.55	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.62	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	0.93	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.56	0.07

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.52	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.56	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	0.87	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.50	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.52	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.47	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	0.76	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.48	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcp	pol	1	3	2	18	0.56	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	lcd	pol	1	3	2	18	0.40	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	lan	pat	pol	1	3	2	18	0.69	0.07
46	Pal	5	agr	0	0	725.42	pla	her	pla	aut	top	pro	pol	1	3	2	18	0.48	0.07
47	Afr	12	for	0	0	1437.80	pla	her	pla	aut	cli	cli	pol	0	4	3	9	-0.54	0.17
48	Afr	10	for	1	1	1479.11	mam	ani	end	mix	veg	pla	plo	1	1	1	9	0.91	0.17
48	Afr	8	for	1	1	1598.25	mam	ani	end	mix	veg	pla	plo	1	1	2	9	1.29	0.17
48	Afr	10	for	1	1	1479.11	mam	ani	end	mix	veg	ved	plo	1	1	1	9	1.02	0.17
48	Afr	8	for	1	1	1598.25	mam	ani	end	mix	veg	ved	plo	1	1	2	9	0.68	0.17
49	Aus	5	for	0	0	1382.87	mam	ani	end	mix	veg	pla	plo	1	1	1	51	0.51	0.02
49	Aus	5	for	0	0	1382.87	mam	ani	end	mix	veg	pla	plo	1	1	1	51	0.24	0.02
49	Aus	5	for	0	0	1382.87	mam	ani	end	mix	lan	lcp	plo	1	1	1	51	0.34	0.02
49	Aus	5	for	0	0	1382.87	mam	ani	end	mix	lan	pat	plo	1	1	1	51	-0.13	0.02
49	Aus	5	for	0	0	1382.87	her	ani	ect	mix	soi	sov	plo	1	1	1	51	0.30	0.02
49	Aus	5	for	0	0	1382.87	her	ani	ect	mix	soi	sod	plo	1	1	1	51	0.21	0.02
49	Aus	5	for	0	0	1382.87	her	ani	ect	mix	lan	lcp	plo	1	1	1	51	0.30	0.02
49	Aus	5	for	0	0	1382.87	her	ani	ect	mix	lan	pat	plo	1	1	1	51	-0.38	0.02
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	lan	lcp	plo	1	3	3	7	1.03	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.84	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.99	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.14	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	1.05	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.23	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.18	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.02	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.09	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.28	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	-0.16	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	1.39	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	1.35	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.67	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.73	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	lan	lcp	plo	1	3	3	7	1.06	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.90	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	1.06	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.18	0.25

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	1.03	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.19	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.22	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.37	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.11	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.30	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	-0.14	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	1.28	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	1.48	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.53	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.78	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	lan	lcp	plo	1	3	3	7	1.18	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	pla	plo	1	3	3	7	0.63	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	pla	plo	1	3	3	7	0.58	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	pla	plo	1	3	3	7	0.26	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	pla	plo	1	3	3	7	2.15	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	pla	plo	1	3	3	7	0.65	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	pla	plo	1	3	3	7	-0.09	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	-0.53	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	0.61	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	0.07	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	-0.07	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	1.03	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	1.01	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	0.50	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	fru	veg	ved	plo	1	3	3	7	0.75	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	lan	lcp	plo	1	3	3	7	0.97	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.18	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.22	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	-0.38	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	1.03	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	0.41	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	pla	plo	1	3	3	7	-0.37	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	-0.29	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	-0.46	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.20	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.20	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.83	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.63	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	1.13	0.25
50	Neo	8	for	0	1	1729.65	bir	ani	end	mix	veg	ved	plo	1	3	3	7	0.32	0.25
51	Neo	9	gra	0	1	1747.69	inv	ani	ect	her	veg	pla	tra	0	1	1	12	0.68	0.11
51	Neo	9	gra	0	1	1747.69	inv	ani	ect	her	veg	pla	tra	0	1	1	12	1.23	0.11
51	Neo	9	gra	0	1	1747.69	inv	ani	ect	her	veg	pla	tra	0	1	1	12	0.79	0.11

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
51	Neo	9	gra	0	1	1747.69	inv	ani	ect	her	veg	pla	tra	0	1	1	12	0.79	0.11
52	Pal	3	mon	0	0	1087.58	inv	ani	ect	mix	veg	pla	plo	1	1	2	60	0.38	0.02
52	Pal	3	mon	0	0	1087.58	inv	ani	ect	mix	veg	pla	plo	1	1	2	6	1.00	0.33
52	Pal	3	mon	0	0	1087.58	inv	ani	ect	mix	veg	pla	plo	1	1	2	12	0.44	0.11
52	Pal	3	mon	0	0	1087.58	inv	ani	ect	mix	veg	ved	plo	1	1	2	6	0.10	0.33
52	Pal	3	mon	0	0	1087.58	inv	ani	ect	mix	veg	ved	plo	1	1	2	12	0.00	0.11
52	Pal	3	mon	0	0	1087.58	inv	ani	ect	mix	veg	ved	plo	1	1	2	60	0.39	0.02
53	Pal	3	for	1	0	921.56	inv	ani	ect	her	veg	pla	plo	1	1	2	16	0.85	0.08
53	Pal	3	for	1	0	921.56	inv	ani	ect	car	veg	pla	plo	1	1	2	16	-0.21	0.08
54	Pal	12	mix	0	0	732.66	bir	ani	end	mix	lan	lcd	gri	1	4	3	328	0.33	0.00
55	Pal	5	mix	1	0	523.72	bir	ani	end	mix	lan	lcd	isl	0	2	1	44	1.58	0.02
55	Pal	5	mix	1	0	523.72	bir	ani	end	mix	lan	lcd	isl	0	2	1	44	1.09	0.02
56	Afr	12	mix	1	1	1372.95	bir	ani	end	mix	top	ele	isl	0	4	3	5	1.37	0.50
57	mix	12	mix	1	1	1533.90	bir	ani	end	mix	top	ele	isl	0	4	4	22	1.16	0.05
57	Oce	12	mix	1	1	1497.67	bir	ani	end	mix	top	ele	isl	0	4	4	25	0.85	0.05
57	Neo	12	mix	1	1	1556.33	bir	ani	end	mix	top	ele	isl	0	4	4	12	0.54	0.11
58	Pal	5	mix	1	0	550.28	pla	mix	pla	aut	lan	lcd	isl	0	2	1	82	1.06	0.01
58	Pal	5	mix	1	0	559.30	pla	mix	pla	aut	lan	lcd	isl	0	2	1	78	1.50	0.01
59	Nea	6	for	0	0	993.07	pla	mix	pla	aut	mix	mix	plo	1	1	2	20	0.51	0.06
59	Nea	6	for	0	0	1115.38	pla	mix	pla	aut	mix	mix	plo	1	1	2	10	1.57	0.14
60	Neo	2	mix	1	1	1304.57	bir	ani	end	mix	veg	pla	isl	0	4	3	15	1.60	0.08
60	Neo	2	mix	1	1	1304.57	bir	ani	end	mix	veg	pla	isl	0	4	3	15	1.21	0.08
60	Neo	2	mix	1	1	1304.57	bir	ani	end	mix	veg	pla	isl	0	4	3	15	1.27	0.08
60	Neo	2	mix	1	1	1304.57	bir	ani	end	mix	top	ele	isl	0	4	3	15	1.24	0.08
61	Nea	12	mix	0	0	1325.23	inv	ani	ect	her	veg	pla	pol	0	4	3	93	0.45	0.01
61	Nea	12	mix	0	0	1325.23	inv	ani	ect	her	veg	pla	pol	0	4	3	93	0.66	0.01
61	Nea	12	mix	0	0	1325.23	inv	ani	ect	her	veg	pla	pol	0	4	3	93	0.69	0.01
62	Aus	12	mix	1	1	1516.45	pla	mix	pla	aut	top	ele	isl	0	2	3	82	0.83	0.01
63	Neo	12	mix	1	1	1389.92	her	ani	ect	car	lan	lcd	isl	0	4	3	33	0.93	0.03
64	Neo	10	for	0	1	1359.00	pla	her	pla	aut	veg	ved	plo	1	1	1	6	0.11	0.33
65	Pal	5	agr	0	0	697.18	pla	mix	pla	aut	top	pro	pol	1	2	2	12	1.50	0.11
65	Pal	5	agr	0	0	697.18	pla	mix	pla	aut	top	ele	pol	1	2	2	12	1.08	0.11
66	Neo	10	for	0	1	1251.73	pla	shr	pla	aut	soi	sov	plo	1	1	1	15	0.97	0.08
66	Neo	10	for	0	1	1251.73	pla	shr	pla	aut	soi	sov	plo	1	1	1	15	0.59	0.08
66	Neo	10	for	0	1	1251.73	pla	shr	pla	aut	soi	sov	plo	1	1	1	15	0.42	0.08
66	Neo	10	for	0	1	1251.73	pla	shr	pla	aut	soi	sov	plo	1	1	1	15	0.79	0.08
67	Pal	5	mix	0	0	684.66	pla	mix	pla	aut	lan	lcd	gri	1	3	2	89	0.78	0.01
68	Neo	12	mix	0	1	1610.14	mam	ani	end	omn	lan	lcd	plo	1	1	1	10	0.59	0.14
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	0.93	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	0.28	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	-0.05	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	0.33	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	pla	plo	1	1	3	6	0.16	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	pla	plo	1	1	3	6	0.62	0.33

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	pla	plo	1	1	3	6	-0.81	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	-0.46	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	0.13	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	0.09	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	0.00	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	pla	plo	1	1	3	6	-0.31	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	pla	plo	1	1	3	6	-0.09	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	pla	plo	1	1	3	6	0.40	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	0.17	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	0.55	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	-0.50	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	vec	plo	1	1	3	6	-0.51	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	pla	plo	1	1	3	6	0.79	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	pla	plo	1	1	3	6	0.30	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	mix	veg	pla	plo	1	1	3	6	-0.29	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	0.23	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	-0.04	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	-0.46	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	vec	plo	1	1	3	6	-0.08	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	pla	plo	1	1	3	6	0.18	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	pla	plo	1	1	3	6	-0.04	0.33
69	Pal	5	agr	1	0	616.09	inv	ani	ect	car	veg	pla	plo	1	1	3	6	0.20	0.33
70	Pal	5	for	1	0	1035.20	pla	shr	pla	aut	top	ele	pol	0	3	2	5	0.31	0.50
70	Pal	5	for	1	0	1035.20	pla	shr	pla	aut	top	ele	pol	0	3	2	5	0.33	0.50
70	Pal	5	for	1	0	1035.20	pla	her	pla	aut	top	ele	pol	0	3	2	5	0.63	0.50
70	Pal	5	for	1	0	1035.20	pla	her	pla	aut	top	ele	pol	0	3	2	5	0.73	0.50
71	Pal	4	mix	0	0	1020.49	pla	mix	pla	aut	lan	lcd	plo	1	2	1	22	0.87	0.05
72	Pal	3	mix	0	0	1073.69	inv	ani	ect	car	veg	vec	plo	1	2	2	15	0.61	0.08
72	Pal	3	mix	0	0	1073.69	inv	ani	ect	car	veg	vec	plo	1	2	2	15	0.62	0.08
72	Pal	3	mix	0	0	1073.69	inv	ani	ect	car	veg	vec	plo	1	2	2	15	0.69	0.08
73	Pal	12	mix	1	0	601.03	pla	mix	pla	aut	top	ele	isl	0	4	3	42	0.73	0.03
73	Pal	12	mix	1	0	601.03	pla	mix	pla	aut	soi	sod	isl	0	4	3	42	1.03	0.03
74	Nea	12	for	0	0	1141.83	bir	ani	end	mix	top	ele	plo	0	4	4	31	0.49	0.04
74	Nea	12	for	0	0	1141.83	bir	ani	end	mix	veg	pla	plo	0	4	4	31	1.90	0.04
75	Nea	5	mix	0	0	998.33	mam	ani	end	mix	top	ele	gri	1	4	3	211	0.55	0.00
76	Pal	5	mix	1	0	544.95	pla	her	pla	aut	lan	lcd	isl	0	2	2	32	1.42	0.03
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	top	ele	isl	0	3	3	201	0.98	0.01
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	soi	sod	isl	0	3	3	201	0.53	0.01
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	top	ele	isl	0	3	3	64	0.79	0.02
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	soi	sod	isl	0	3	3	64	0.32	0.02
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	top	ele	isl	0	3	3	35	0.84	0.03
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	soi	sod	isl	0	3	3	35	0.37	0.03
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	top	ele	isl	0	3	3	19	1.11	0.06
77	Pal	3	mix	1	0	1054.96	pla	mix	pla	aut	soi	sod	isl	0	3	3	19	0.55	0.06

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
78	Nea	7	for	0	0	1060.26	bir	ani	end	mix	veg	vec	plo	0	2	1	4	1.68	1.00
78	Nea	9	gra	0	0	1431.32	bir	ani	end	mix	veg	vec	plo	0	2	3	4	-0.72	1.00
78	Neo	10	mix	0	1	1497.37	bir	ani	end	mix	veg	vec	plo	0	2	1	7	2.25	0.25
79	Pal	3	mix	0	0	890.62	bir	ani	end	omn	veg	vec	plo	0	2	1	16	0.41	0.08
80	Afr	12	xer	0	0	1390.63	mam	ani	end	mix	veg	vec	plo	1	1	3	6	1.38	0.33
80	Afr	12	xer	0	0	1390.63	mam	ani	end	mix	veg	vec	plo	1	1	3	6	2.18	0.33
80	Afr	12	xer	0	0	1390.63	mam	ani	end	mix	veg	vec	plo	1	1	3	6	1.51	0.33
80	Afr	12	xer	0	0	1390.63	mam	ani	end	mix	veg	vec	plo	1	1	3	6	1.61	0.33
80	Afr	12	xer	0	0	1390.63	mam	ani	end	mix	veg	vec	plo	1	1	3	6	2.44	0.33
80	Afr	12	xer	0	0	1390.63	mam	ani	end	mix	top	mic	plo	1	1	3	6	2.21	0.33
81	Nea	12	mix	0	0	1217.72	mam	ani	end	mix	top	ele	gri	0	4	4	130	1.12	0.01
81	Nea	12	mix	0	0	516.77	mam	ani	end	mix	top	ele	gri	0	4	4	206	0.31	0.00
81	Nea	12	mix	0	0	1217.72	mam	ani	end	mix	cli	cli	gri	0	4	4	130	0.36	0.01
81	Nea	12	mix	0	0	516.77	mam	ani	end	mix	cli	cli	gri	0	4	4	206	0.18	0.00
81	Nea	12	mix	0	0	1217.72	mam	ani	end	mix	cli	cli	gri	0	4	4	130	0.72	0.01
81	Nea	12	mix	0	0	516.77	mam	ani	end	mix	cli	cli	gri	0	4	4	206	0.61	0.00
82	Nea	12	mix	0	0	712.01	inv	ani	ect	mix	cli	cli	gri	0	4	4	336	0.54	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	mix	top	ele	gri	0	4	4	1737	0.44	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	mix	lan	lcd	gri	0	4	4	1737	0.81	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	mix	veg	pla	gri	0	4	4	1737	0.68	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	fru	top	ele	gri	0	4	4	1737	0.19	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	fru	lan	lcd	gri	0	4	4	1737	0.65	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	fru	veg	pla	gri	0	4	4	1737	1.42	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	fru	top	ele	gri	0	4	4	1737	0.35	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	fru	lan	lcd	gri	0	4	4	1737	0.83	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	fru	veg	pla	gri	0	4	4	1737	0.91	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	mix	top	ele	gri	0	4	4	1737	0.39	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	mix	lan	lcd	gri	0	4	4	1737	0.79	0.00
84	Afr	12	mix	0	1	1836.67	bir	ani	end	mix	veg	pla	gri	0	4	4	1737	0.73	0.00
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	top	ele	gri	1	4	3	160	0.68	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	lan	lcd	gri	1	4	3	160	0.65	0.01
83	Afr	12	mix	0	1	1885.53	pla	shr	pla	aut	top	ele	gri	1	4	3	160	0.58	0.01
83	Afr	12	mix	0	1	1885.53	pla	shr	pla	aut	lan	lcd	gri	1	4	3	160	0.68	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.13	0.01
83	Afr	12	mix	0	1	1885.53	pla	shr	pla	aut	top	ele	gri	1	4	3	160	0.56	0.01
83	Afr	12	mix	0	1	1885.53	pla	shr	pla	aut	lan	lcd	gri	1	4	3	160	0.68	0.01
83	Afr	12	mix	0	1	1885.53	pla	shr	pla	aut	top	ele	gri	1	4	3	160	0.58	0.01
83	Afr	12	mix	0	1	1885.53	pla	shr	pla	aut	lan	lcd	gri	1	4	3	160	0.63	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.07	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.10	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	0.81	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	top	ele	gri	1	4	3	160	0.69	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	lan	lcd	gri	1	4	3	160	0.74	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	1.26	0.01

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	1.26	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	1.19	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	0.91	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	top	ele	gri	1	4	3	160	0.71	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	lan	lcd	gri	1	4	3	160	0.68	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	1.16	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	1.16	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	1.13	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	fru	veg	pla	gri	1	4	3	160	0.85	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	top	ele	gri	1	4	3	160	0.69	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	lan	lcd	gri	1	4	3	160	0.63	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.05	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.00	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.07	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	0.76	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	top	ele	gri	1	4	3	160	0.65	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	lan	lcd	gri	1	4	3	160	0.63	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.07	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.05	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	1.07	0.01
83	Afr	12	mix	0	1	1885.53	bir	ani	end	mix	veg	pla	gri	1	4	3	160	0.79	0.01
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	veg	pla	pol	0	3	3	22	0.45	0.05
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	lan	lcd	pol	0	3	3	22	0.30	0.05
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	lan	lcd	pol	0	3	3	22	0.62	0.05
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	veg	vec	pol	0	3	3	22	0.63	0.05
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	veg	pla	pol	0	3	3	22	0.71	0.05
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	lan	lcd	pol	0	3	3	22	0.41	0.05
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	lan	lcd	pol	0	3	3	22	0.74	0.05
85	Aus	12	mix	0	0	1535.42	mam	ani	end	mix	veg	vec	pol	0	3	3	22	0.81	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	veg	pla	pol	0	3	3	22	0.84	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	lan	lcd	pol	0	3	3	22	0.77	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	lan	lcd	pol	0	3	3	22	0.71	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	veg	vec	pol	0	3	3	22	0.77	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	veg	pla	pol	0	3	3	22	0.59	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	lan	lcd	pol	0	3	3	22	0.42	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	lan	lcd	pol	0	3	3	22	0.68	0.05
85	Aus	12	mix	0	0	1535.42	bir	ani	end	mix	veg	vec	pol	0	3	3	22	0.76	0.05
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	veg	pla	pol	0	3	3	22	0.78	0.05
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	lan	lcd	pol	0	3	3	22	1.04	0.05
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	lan	lcd	pol	0	3	3	22	0.64	0.05
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	veg	vec	pol	0	3	3	22	0.66	0.05
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	veg	pla	pol	0	3	3	22	0.71	0.05
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	lan	lcd	pol	0	3	3	22	0.42	0.05
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	lan	lcd	pol	0	3	3	22	0.81	0.05

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
85	Aus	12	mix	0	0	1535.42	her	ani	ect	mix	veg	vec	pol	0	3	3	22	0.66	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	veg	pla	pol	0	3	3	22	0.85	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	lan	lcd	pol	0	3	3	22	0.52	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	lan	lcd	pol	0	3	3	22	0.94	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	veg	vec	pol	0	3	3	22	0.95	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	veg	pla	pol	0	3	3	22	0.90	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	lan	lcd	pol	0	3	3	22	0.90	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	lan	lcd	pol	0	3	3	22	0.83	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	veg	vec	pol	0	3	3	22	0.89	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	veg	pla	pol	0	3	3	22	1.12	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	lan	lcd	pol	0	3	3	22	0.85	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	lan	lcd	pol	0	3	3	22	1.12	0.05
85	Aus	12	mix	0	0	1535.42	mix	ani	mix	mix	veg	vec	pol	0	3	3	22	1.16	0.05
86	mix	12	mix	0	0	1004.49	inv	ani	ect	her	top	ele	plo	1	4	4	1822	0.11	0.00
87	Ind	10	for	1	1	1539.12	pla	mix	pla	aut	lan	lcd	isl	0	2	1	17	0.32	0.07
87	Ind	10	for	1	1	1539.12	pla	mix	pla	aut	top	ele	isl	0	2	1	17	0.35	0.07
87	Ind	10	for	1	1	1539.12	inv	ani	ect	her	lan	lcd	isl	0	2	1	17	0.51	0.07
87	Ind	10	for	1	1	1539.12	inv	ani	ect	her	top	ele	isl	0	2	1	17	-0.05	0.07
87	Ind	10	for	1	1	1539.12	bir	ani	end	mix	lan	lcd	isl	0	2	1	17	0.51	0.07
87	Ind	10	for	1	1	1539.12	bir	ani	end	mix	top	ele	isl	0	2	1	17	0.40	0.07
88	Pal	5	mix	1	0	394.73	pla	mix	pla	aut	lan	lcd	isl	0	2	1	47	1.77	0.02
89	Pal	5	mix	1	0	549.96	inv	ani	ect	mix	lan	lcd	isl	0	3	1	24	0.25	0.05
91	Pal	5	gra	0	0	723.19	inv	ani	ect	her	lan	lcd	pol	0	2	2	32	0.47	0.03
90	Pal	5	gra	0	0	723.19	pla	mix	pla	aut	lan	lcd	pol	1	2	2	31	0.16	0.04
93	Neo	12	mix	0	1	1615.10	pla	shr	pla	aut	top	ele	gri	0	4	4	6638	0.01	0.00
93	Neo	12	mix	0	1	1615.10	pla	shr	pla	aut	top	ele	gri	0	4	4	119	0.29	0.01
92	mix	12	mix	1	1	1068.93	pla	mix	pla	aut	top	ele	isl	0	3	4	488	0.72	0.00
92	mix	12	mix	0	1	1113.77	pla	mix	pla	aut	top	ele	pol	0	4	4	970	0.50	0.00
92	mix	12	mix	0	1	1068.93	pla	mix	pla	aut	top	ele	pol	0	4	4	1458	0.85	0.00
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	top	pro	pol	1	3	1	79	-0.51	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	top	mic	pol	1	2	1	79	-0.46	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	top	pro	pol	1	2	1	79	0.30	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.24	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.33	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	2	1	79	0.31	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.30	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.22	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.39	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	2	1	79	0.29	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.23	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.27	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.23	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	2	1	79	0.29	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.32	0.01

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.45	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.38	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	2	1	79	0.46	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.30	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.23	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.26	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	2	1	79	0.20	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.24	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.30	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.39	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	2	1	79	0.39	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	2	1	79	0.32	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	3	1	79	0.23	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	3	1	79	0.24	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	3	1	79	0.27	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	3	1	79	0.23	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	3	1	79	0.23	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	3	1	79	0.31	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	lcd	pol	1	3	1	79	0.29	0.01
95	Nea	12	mix	0	0	716.19	pla	mix	pla	aut	lan	pat	pol	1	3	1	79	0.08	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	veg	pla	plo	1	1	2	76	0.45	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcd	gri	1	2	2	76	-0.38	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.39	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.14	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.21	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.30	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.32	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.30	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.26	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.12	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	3	2	76	-0.29	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	mic	pol	1	3	2	76	0.44	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.37	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.23	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.22	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.31	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.33	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.32	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.18	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.07	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	3	2	76	-0.26	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.37	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.29	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.24	0.01

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.38	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.32	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.34	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.24	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.01	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	3	2	76	-0.31	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.33	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.29	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.18	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.29	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.32	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.35	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.17	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	-0.05	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	3	2	76	-0.31	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.32	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.28	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.17	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.27	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.34	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.34	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.17	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	-0.06	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	3	2	76	-0.31	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.37	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.28	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.28	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.24	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.37	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.31	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.19	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.08	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	3	2	76	-0.31	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.35	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.28	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.30	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.04	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	3	2	76	0.34	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.40	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.23	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	3	2	76	0.23	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	3	2	76	-0.30	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	2	2	76	0.51	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	2	2	76	0.35	0.01

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	2	2	76	0.48	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	2	2	76	-0.10	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	pat	pol	1	2	2	76	0.42	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	2	2	76	0.42	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	2	2	76	0.27	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	lan	lcp	pol	1	2	2	76	0.34	0.01
94	Nea	12	mix	0	0	716.19	inv	ani	ect	her	top	pro	pol	1	2	2	76	-0.24	0.01
96	Neo	9	gra	0	1	1539.37	inv	ani	ect	her	veg	pla	tra	0	1	2	24	1.27	0.05
96	Neo	9	gra	0	1	1539.37	inv	ani	ect	her	veg	pla	tra	0	1	2	20	0.59	0.06
96	Neo	9	gra	0	1	1539.37	inv	ani	ect	her	veg	pla	tra	0	1	2	24	1.06	0.05
96	Neo	9	gra	0	1	1539.37	inv	ani	ect	her	veg	pla	tra	0	1	2	24	0.62	0.05
96	Neo	9	gra	0	1	1539.37	inv	ani	ect	her	veg	pla	tra	0	1	2	24	0.79	0.05
96	Neo	9	gra	0	1	1539.37	inv	ani	ect	her	veg	pla	tra	0	1	2	20	0.68	0.06
97	Aus	5	for	0	0	1200.24	inv	ani	ect	omn	veg	vec	plo	1	1	1	28	-0.58	0.04
97	Aus	5	for	0	0	1200.24	inv	ani	ect	omn	veg	vec	plo	1	1	1	28	-0.48	0.04
97	Aus	5	for	0	0	1200.24	inv	ani	ect	omn	soi	sov	plo	1	1	1	28	-0.47	0.04
97	Aus	5	for	0	0	1200.24	inv	ani	ect	omn	veg	ved	plo	1	1	1	28	-0.41	0.04
98	Aus	5	for	0	0	1200.24	inv	ani	ect	mix	veg	vec	plo	1	1	1	28	0.58	0.04
98	Aus	5	for	0	0	1200.24	inv	ani	ect	mix	veg	vec	plo	1	1	1	28	0.45	0.04
98	Aus	5	for	0	0	1200.24	inv	ani	ect	mix	veg	vec	plo	1	1	1	28	0.50	0.04
98	Aus	5	for	0	0	1200.24	inv	ani	ect	mix	soi	sov	plo	1	1	1	28	0.69	0.04
99	Nea	5	for	0	0	810.46	pla	mix	pla	aut	veg	ved	plo	1	1	2	30	0.32	0.04
99	Nea	5	for	0	0	810.46	pla	mix	pla	aut	soi	sov	plo	1	1	2	30	-0.04	0.04
99	Nea	5	for	0	0	810.46	pla	mix	pla	aut	soi	sov	plo	1	1	2	30	0.29	0.04
99	Nea	5	for	0	0	810.46	pla	mix	pla	aut	soi	sov	plo	1	1	2	30	-0.15	0.04
99	Nea	5	for	0	0	810.46	pla	mix	pla	aut	cli	cli	plo	1	1	2	30	-0.05	0.04
100	Pal	12	mix	1	0	602.28	bir	ani	end	mix	lan	lcd	gri	1	3	3	2362	0.06	0.00
100	Pal	12	mix	1	0	602.28	bir	ani	end	mix	lan	lcd	gri	1	3	3	2362	0.07	0.00
101	Pal	3	for	0	0	1167.31	pla	mix	pla	aut	lan	lcd	plo	1	1	1	32	1.00	0.03
102	Afr	3	for	0	0	1278.93	pla	mix	pla	aut	top	ele	gri	1	4	3	55	0.88	0.02
102	Afr	3	for	0	0	1278.93	pla	mix	pla	aut	cli	cli	gri	1	4	3	55	0.87	0.02
102	Afr	3	for	0	0	1278.93	pla	mix	pla	aut	lan	lcd	gri	1	4	3	55	0.31	0.02
102	Afr	3	for	0	0	1278.93	pla	mix	pla	aut	soi	sod	gri	1	4	3	55	0.27	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	top	ele	gri	1	4	3	55	0.68	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	cli	cli	gri	1	4	3	55	0.86	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	lan	lcd	gri	1	4	3	55	0.18	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	soi	sod	gri	1	4	3	55	0.36	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	top	ele	gri	1	4	3	55	0.96	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	cli	cli	gri	1	4	3	55	1.18	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	lan	lcd	gri	1	4	3	55	0.24	0.02
102	Afr	3	for	0	0	1278.93	pla	her	pla	aut	soi	sod	gri	1	4	3	55	0.17	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	top	ele	gri	1	4	3	55	0.87	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	cli	cli	gri	1	4	3	55	1.03	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	lan	lcd	gri	1	4	3	55	0.34	0.02

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	soi	sod	gri	1	4	3	55	0.21	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	top	ele	gri	1	4	3	55	0.76	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	cli	cli	gri	1	4	3	55	0.71	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	lan	lcd	gri	1	4	3	55	0.32	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	soi	sod	gri	1	4	3	55	0.33	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	top	ele	gri	1	4	3	55	0.79	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	cli	cli	gri	1	4	3	55	0.68	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	lan	lcd	gri	1	4	3	55	0.32	0.02
102	Afr	3	for	0	0	1278.93	pla	shr	pla	aut	soi	sod	gri	1	4	3	55	0.21	0.02
103	Pal	12	mix	0	0	1048.25	pla	mix	pla	aut	top	ele	gri	1	4	3	254	0.95	0.00
104	mix	10	mix	1	1	1476.35	her	ani	ect	mix	top	ele	isl	0	4	4	48	0.39	0.02
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	3	1	29	-0.58	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	3	1	29	0.17	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	3	1	29	-0.14	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	pat	pol	1	3	1	29	0.26	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcd	pol	1	3	1	29	0.52	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	-0.26	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	0.16	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	-0.09	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	pat	pol	1	2	1	29	-0.13	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcd	pol	1	2	1	29	0.23	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	-0.34	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	-0.13	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	-0.12	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	pat	pol	1	2	1	29	0.17	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcd	pol	1	2	1	29	0.33	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	-0.50	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	0.21	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	2	1	29	0.15	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	pat	pol	1	2	1	29	0.21	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcd	pol	1	2	1	29	0.47	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	3	1	29	-0.83	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	3	1	29	0.22	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcp	pol	1	3	1	29	-0.20	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	pat	pol	1	3	1	29	-0.14	0.04
105	Pal	1	agr	0	0	536.01	pla	mix	pla	aut	lan	lcd	pol	1	3	1	29	0.79	0.04
106	Pal	5	mix	0	0	704.96	inv	ani	ect	her	lan	lcd	gri	1	3	3	197	0.43	0.01
109	Pal	6	mix	0	0	617.76	pla	mix	pla	aut	lan	lcd	gri	1	3	2	156	0.54	0.01
107	Pal	3	agr	0	0	991.11	inv	ani	ect	mix	lan	lcd	tra	0	1	1	35	0.65	0.03
107	Pal	3	agr	0	0	991.11	inv	ani	ect	mix	lan	lcd	tra	0	1	1	35	0.38	0.03
107	Pal	3	agr	0	0	991.11	inv	ani	ect	mix	lan	lcd	tra	0	1	1	35	0.76	0.03
108	Pal	12	mix	0	0	806.39	pla	her	pla	aut	lan	lcd	gri	1	3	3	1476	1.03	0.00
108	Pal	12	mix	0	0	806.39	pla	her	pla	aut	top	ele	gri	1	3	3	1476	0.82	0.00
110	Neo	12	for	0	1	1571.91	bir	ani	end	mix	top	pro	pol	0	3	2	13	0.29	0.10

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
110	Neo	12	for	0	1	1571.91	bir	ani	end	mix	top	ele	pol	0	3	2	13	0.86	0.10
111	Pal	3	mix	1	0	908.75	pla	mix	pla	aut	lan	lcd	isl	0	2	2	14	1.57	0.09
112	Neo	10	for	0	1	1669.63	mam	ani	end	mix	top	ele	pol	0	4	4	9	-0.20	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	mix	top	ele	pol	0	4	4	9	0.06	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	mix	top	ele	pol	0	4	4	9	-0.05	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	fru	top	ele	pol	0	4	4	9	-0.41	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	ins	top	ele	pol	0	4	4	9	-0.40	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	her	top	ele	pol	0	4	4	9	-0.15	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	car	top	ele	pol	0	4	4	9	-0.20	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	fru	top	ele	pol	0	4	4	9	0.19	0.17
112	Neo	10	for	0	1	1669.63	mam	ani	end	her	top	ele	pol	0	4	4	9	-0.18	0.17
113	Neo	12	xer	0	0	1214.31	mam	ani	end	mix	veg	pla	plo	0	1	3	9	1.02	0.17
113	Neo	12	xer	0	0	1214.31	mam	ani	end	mix	veg	pla	plo	0	1	3	9	1.33	0.17
113	Neo	12	xer	0	0	1214.31	mam	ani	end	mix	veg	vec	plo	0	1	3	9	0.83	0.17
113	Neo	12	xer	0	0	1214.31	mam	ani	end	mix	veg	vec	plo	0	1	3	9	1.66	0.17
113	Neo	12	xer	0	0	1214.31	mam	ani	end	mix	veg	vec	plo	0	1	3	9	0.91	0.17
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	2	2	32	0.38	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	veg	pla	pol	0	1	2	32	0.77	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	2	2	32	0.31	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.23	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.12	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.05	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.03	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.05	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.05	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.02	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.00	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	0.02	0.03
114	Pal	5	gra	0	0	723.19	inv	ani	ect	mix	lan	lcd	pol	1	3	2	32	-0.01	0.03
115	Pal	1	for	0	0	562.84	pla	shr	pla	aut	lan	lcd	plo	0	2	1	42	0.28	0.03
115	Pal	5	for	0	0	574.60	pla	shr	pla	aut	soi	sod	plo	0	2	1	44	0.48	0.02
115	Pal	5	for	0	0	574.60	pla	her	pla	aut	soi	sod	plo	0	2	1	44	0.32	0.02
116	Pal	12	mix	1	0	880.26	mam	ani	end	mix	top	ele	isl	0	4	4	12	1.18	0.11
117	Afr	12	gra	0	0	1469.26	mam	ani	end	mix	top	ele	plo	0	3	3	39	0.18	0.03
117	Afr	12	gra	0	0	1469.26	mam	ani	end	mix	top	ele	plo	0	3	3	39	0.27	0.03
118	Nea	3	for	0	0	1225.34	pla	shr	pla	aut	top	pro	plo	0	2	1	175	0.24	0.01
119	Pal	3	mix	0	0	1158.75	her	ani	ect	mix	top	ele	gri	1	3	3	158	0.20	0.01
119	Pal	3	mix	0	0	1158.75	her	ani	ect	mix	lan	lcd	gri	1	3	3	158	0.19	0.01
119	Pal	3	mix	0	0	1158.75	her	ani	ect	mix	top	ele	gri	1	3	3	158	0.29	0.01
119	Pal	3	mix	0	0	1158.75	her	ani	ect	mix	lan	lcd	gri	1	3	3	158	0.28	0.01
119	Pal	3	mix	0	0	1158.75	mam	ani	end	mix	top	ele	gri	1	3	3	158	0.52	0.01
119	Pal	3	mix	0	0	1158.75	mam	ani	end	mix	lan	lcd	gri	1	3	3	158	0.48	0.01
119	Pal	3	mix	0	0	1158.75	bir	ani	end	mix	top	ele	gri	1	3	3	158	0.29	0.01
119	Pal	3	mix	0	0	1158.75	bir	ani	end	mix	lan	lcd	gri	1	3	3	158	0.41	0.01

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
119	Pal	3	mix	0	0	1158.75	mix	ani	mix	mix	top	ele	gri	1	3	3	158	0.45	0.01
119	Pal	3	mix	0	0	1158.75	mix	ani	mix	mix	lan	lcd	gri	1	3	3	158	0.54	0.01
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.71	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.83	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	-0.74	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.63	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.63	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	-0.66	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	-0.74	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	-0.87	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.39	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	-0.41	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.76	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	-0.63	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.51	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	-0.83	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	0.83	0.04
120	Pal	12	agr	0	0	858.07	pla	mix	pla	aut	lan	pat	plo	1	2	2	30	1.26	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.69	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.66	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	-0.62	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.65	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.65	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	-0.55	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	-0.40	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	-0.56	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.33	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	-0.30	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.63	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	-0.58	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.28	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	-0.68	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.60	0.04
120	Pal	12	agr	0	0	858.07	pla	her	pla	aut	lan	pat	plo	1	2	2	30	0.95	0.04
121	Pal	12	for	0	0	555.82	bir	ani	end	mix	veg	vec	plo	0	2	2	8	0.76	0.20
122	Pal	5	for	1	0	1084.88	pla	mix	pla	aut	top	mic	pol	0	2	1	39	1.07	0.03
122	Pal	5	for	1	0	1084.88	pla	mix	pla	aut	lan	lcd	pol	0	2	1	39	0.60	0.03
123	Nea	12	mix	0	0	985.35	mam	ani	end	mix	top	ele	pol	0	4	4	24	1.07	0.05
123	Nea	12	mix	0	0	985.35	mam	ani	end	mix	lan	lcd	pol	0	4	4	24	0.89	0.05
123	Nea	12	mix	0	0	985.35	mam	ani	end	mix	lan	lcd	pol	0	4	4	24	0.65	0.05
124	Pal	5	for	0	0	589.91	bir	ani	end	mix	veg	ved	plo	1	2	1	8	1.60	0.20
124	Pal	5	for	0	0	589.91	bir	ani	end	mix	veg	ved	plo	1	2	1	8	0.38	0.20
125	Pal	5	for	1	0	595.49	pla	shr	pla	aut	lan	lcd	isl	0	2	1	17	0.32	0.07
125	Pal	5	for	1	0	595.49	inv	ani	ect	mix	lan	lcd	isl	0	2	1	17	0.23	0.07

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
125	Pal	5	for	1	0	595.49	inv	ani	ect	car	lan	lcd	isl	0	2	1	17	0.18	0.07
125	Pal	5	for	1	0	595.49	pla	shr	pla	aut	lan	lcd	isl	0	2	1	17	0.27	0.07
125	Pal	5	for	1	0	595.49	inv	ani	ect	mix	lan	lcd	isl	0	2	1	17	0.18	0.07
125	Pal	5	for	1	0	595.49	inv	ani	ect	car	lan	lcd	isl	0	2	1	17	0.07	0.07
125	Pal	5	for	1	0	595.49	pla	shr	pla	aut	veg	ved	isl	0	2	1	17	-0.54	0.07
125	Pal	5	for	1	0	595.49	inv	ani	ect	mix	veg	ved	isl	0	2	1	17	-0.46	0.07
125	Pal	5	for	1	0	595.49	inv	ani	ect	car	veg	ved	isl	0	2	1	17	-0.56	0.07
126	Afr	9	gra	0	1	2124.68	bir	ani	end	mix	lan	lcd	tra	0	2	3	89	0.54	0.01
126	Afr	9	gra	0	1	2124.68	bir	ani	end	mix	lan	lcd	tra	0	2	3	89	0.35	0.01
127	Afr	12	gra	0	1	1650.87	mam	ani	end	mix	lan	lcd	gri	1	4	2	7	1.54	0.25
127	Afr	12	gra	0	1	1650.87	mam	ani	end	mix	lan	lcd	gri	1	4	2	7	1.38	0.25
128	Pal	1	for	0	0	533.74	inv	ani	ect	her	veg	ved	pol	1	3	1	9	0.88	0.17
128	Pal	1	for	0	0	533.74	inv	ani	ect	her	veg	ved	plo	1	2	1	17	0.77	0.07
128	Pal	1	for	0	0	533.74	inv	ani	ect	her	veg	ved	plo	1	1	1	49	0.54	0.02
129	Afr	9	gra	0	1	1826.91	pla	mix	pla	aut	lan	lcd	plo	1	1	1	60	0.42	0.02
129	Afr	9	gra	0	1	1826.91	pla	mix	pla	aut	lan	lcd	plo	1	1	1	60	0.17	0.02
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	pla	plo	0	2	3	6	0.10	0.33
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	pla	plo	0	2	3	7	0.27	0.25
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	ved	plo	0	2	3	7	-0.30	0.25
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	ved	plo	0	2	3	7	0.84	0.25
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	pla	plo	0	2	3	7	-0.13	0.25
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	pla	plo	0	2	3	6	0.54	0.33
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	ved	plo	0	2	3	4	0.50	1.00
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	ved	plo	0	2	3	5	1.44	0.50
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	ved	plo	0	2	3	5	0.51	0.50
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	vec	plo	0	2	3	7	-0.35	0.25
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	vec	plo	0	2	3	7	-0.71	0.25
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	vec	plo	0	2	3	7	0.75	0.25
130	Neo	10	for	0	1	1490.03	bir	ani	end	mix	veg	vec	plo	0	2	3	7	0.92	0.25
131	Nea	7	gra	0	0	1289.53	pla	mix	pla	aut	lan	lcd	pol	1	1	1	187	0.01	0.01
131	Nea	7	gra	0	0	1289.53	pla	mix	pla	aut	lan	lcd	pol	1	1	1	187	0.08	0.01
131	Nea	7	gra	0	0	1289.53	pla	mix	pla	aut	lan	lcd	pol	1	1	1	187	0.16	0.01
131	Nea	7	gra	0	0	1289.53	pla	mix	pla	aut	lan	lcd	pol	1	1	1	187	0.18	0.01
131	Nea	7	gra	0	0	1289.53	pla	mix	pla	aut	lan	lcd	pol	1	1	1	187	0.23	0.01
131	Nea	7	gra	0	0	1289.53	pla	mix	pla	aut	lan	lcd	pol	1	1	1	187	0.23	0.01
132	Pal	3	mix	1	0	1000.24	pla	mix	pla	aut	lan	lcd	isl	0	2	3	86	0.63	0.01
132	Pal	3	mix	1	0	1000.24	pla	her	pla	aut	lan	lcd	isl	0	2	3	86	0.64	0.01
132	Pal	3	mix	1	0	1000.24	pla	her	pla	aut	lan	lcd	isl	0	2	3	86	0.33	0.01
132	Pal	3	mix	1	0	1000.24	pla	mix	pla	aut	lan	lcd	isl	0	2	3	86	0.44	0.01
132	Pal	3	mix	1	0	1000.24	pla	mix	pla	aut	lan	lcd	isl	0	2	3	86	0.34	0.01
133	Pal	1	for	0	0	438.91	pla	mix	pla	aut	lan	lcd	gri	1	2	1	440	0.42	0.00
133	Pal	1	for	0	0	438.91	pla	mix	pla	aut	lan	lcd	gri	1	2	1	440	0.19	0.00
133	Pal	1	for	0	0	438.91	pla	shr	pla	aut	lan	lcd	gri	1	2	1	440	0.26	0.00
133	Pal	1	for	0	0	438.91	pla	shr	pla	aut	lan	lcd	gri	1	2	1	440	0.03	0.00

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
133	Pal	1	for	0	0	438.91	pla	her	pla	aut	lan	lcd	gri	1	2	1	440	0.44	0.00
133	Pal	1	for	0	0	438.91	pla	her	pla	aut	lan	lcd	gri	1	2	1	440	0.23	0.00
134	mix	10	for	0	1	1686.87	bir	ani	end	mix	veg	vec	plo	0	2	4	6	0.16	0.33
134	mix	10	for	0	1	1686.87	bir	ani	end	fru	veg	vec	plo	0	2	4	6	0.15	0.33
135	Nea	5	for	0	0	1327.17	bir	ani	end	mix	lan	lcd	pol	1	2	1	16	-0.33	0.08
136	Neo	12	for	0	1	1511.51	pla	shr	pla	aut	soi	sov	pol	0	2	3	20	1.16	0.06
136	Neo	12	for	0	1	1511.51	pla	shr	pla	aut	top	ele	pol	0	2	3	20	0.95	0.06
136	Neo	12	for	0	1	1511.51	pla	shr	pla	aut	lan	pat	pol	0	2	3	20	-0.33	0.06
137	Neo	10	agr	0	1	1429.75	inv	ani	ect	omn	veg	vec	plo	1	1	1	10	1.59	0.14
138	Oce	8	mix	1	1	1315.48	her	ani	ect	mix	top	ele	isl	0	2	1	22	0.20	0.05
138	Oce	8	mix	1	1	1315.48	her	ani	ect	mix	veg	vec	isl	0	2	1	22	0.81	0.05
139	Nea	2	xer	0	0	1437.02	her	ani	ect	mix	veg	ved	pol	0	3	3	10	1.40	0.14
140	Afr	2	xer	0	0	1824.52	bir	ani	end	mix	veg	ved	pol	0	1	3	9	0.14	0.17
140	Afr	2	xer	0	0	1824.52	bir	ani	end	mix	veg	ved	pol	0	1	3	9	1.08	0.17
141	Pal	5	for	0	0	643.28	pla	mix	pla	aut	lan	lcd	pol	0	1	1	153	0.08	0.01
142	Neo	10	for	0	1	1332.99	her	ani	ect	mix	veg	vec	pol	0	2	1	10	2.24	0.14
142	Neo	10	for	0	1	1332.99	her	ani	ect	mix	veg	vec	pol	0	2	1	10	0.19	0.14
143	Neo	9	agr	0	0	1381.55	pla	mix	pla	aut	lan	pat	pol	0	3	2	10	1.18	0.14
143	Neo	9	agr	0	0	1381.55	pla	mix	pla	aut	lan	pat	pol	0	3	2	10	0.96	0.14
144	Pal	5	for	0	0	544.61	bir	ani	end	mix	veg	pla	plo	1	1	3	168	0.85	0.01
144	Pal	5	for	0	0	544.61	bir	ani	end	mix	veg	ved	plo	1	1	3	168	0.02	0.01
145	Nea	3	for	1	0	1386.92	bir	ani	end	mix	top	ele	isl	0	3	3	16	0.87	0.08
145	Nea	3	for	1	0	1386.92	bir	ani	end	mix	veg	pla	isl	0	3	3	16	1.22	0.08
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	0.50	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	-0.47	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	0.54	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	0.74	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	1.42	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	0.17	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	0.33	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	-0.07	0.12
146	Neo	12	mix	1	1	1604.60	pla	mix	pla	aut	lan	lcd	isl	0	4	2	11	-0.55	0.12
147	Pal	5	agr	0	0	725.42	inv	ani	ect	car	lan	lcp	pol	1	3	2	24	0.63	0.05
148	mix	12	mix	0	0	913.02	mam	ani	end	mix	veg	pla	pol	0	4	4	28	0.89	0.04
148	mix	12	mix	0	0	913.02	bir	ani	end	mix	veg	pla	pol	0	4	4	28	1.03	0.04
148	mix	12	mix	0	0	913.02	her	ani	ect	mix	veg	pla	pol	0	4	4	28	1.19	0.04
148	mix	12	mix	0	0	913.02	her	ani	ect	mix	veg	pla	pol	0	4	4	28	1.26	0.04
148	mix	12	mix	0	0	913.02	mam	ani	end	mix	top	ele	pol	0	4	4	28	0.83	0.04
148	mix	12	mix	0	0	913.02	bir	ani	end	mix	top	ele	pol	0	4	4	28	0.38	0.04
148	mix	12	mix	0	0	913.02	her	ani	ect	mix	top	ele	pol	0	4	4	28	0.09	0.04
148	mix	12	mix	0	0	913.02	her	ani	ect	mix	top	ele	pol	0	4	4	28	0.15	0.04
149	Neo	12	mix	0	0	1270.50	bir	ani	end	mix	top	ele	gri	1	4	4	336	-0.46	0.00
149	Neo	12	mix	0	0	1270.50	bir	ani	end	mix	veg	vec	gri	1	4	4	336	0.76	0.00
149	Neo	12	mix	0	0	1270.50	bir	ani	end	mix	veg	vec	gri	1	4	4	336	0.81	0.00

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.27	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.00	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.50	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.63	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.52	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.73	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.47	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.42	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.55	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.65	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.00	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	-0.39	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.27	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.00	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.50	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.67	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.51	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.77	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.47	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.51	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.54	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	0.69	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	lan	lcd	gri	0	4	4	1676	0.00	0.00
150	Neo	12	mix	0	1	1553.81	bir	ani	end	mix	top	ele	gri	0	4	4	1676	-0.47	0.00
151	Pal	5	mix	1	0	600.47	bir	ani	end	mix	lan	lcd	isl	0	3	3	73	1.33	0.01
151	Pal	5	mix	1	0	600.47	bir	ani	end	mix	top	ele	isl	0	3	3	73	0.49	0.01
151	Pal	12	mix	1	0	599.44	bir	ani	end	mix	lan	lcd	isl	0	3	3	61	1.30	0.02
151	Pal	12	mix	1	0	599.44	bir	ani	end	mix	top	ele	isl	0	3	3	61	0.47	0.02
152	Pal	12	mix	0	0	1048.25	pla	mix	pla	aut	top	ele	pol	0	4	3	93	0.20	0.01
153	Neo	9	gra	0	1	1553.94	inv	ani	ect	mix	veg	pla	plo	1	1	1	30	0.41	0.04
154	Nea	12	mix	0	0	1325.23	pla	mix	pla	aut	top	ele	pol	0	4	3	93	0.75	0.01
155	Neo	12	mix	1	1	1389.92	bir	ani	end	mix	top	ele	isl	0	4	3	19	0.80	0.06
155	Neo	12	mix	1	1	1389.92	bir	ani	end	mix	lan	lcd	isl	0	4	3	19	0.95	0.06
155	Neo	12	mix	1	1	1389.92	mam	ani	end	mix	top	ele	isl	0	4	3	15	0.24	0.08
155	Neo	12	mix	1	1	1389.92	mam	ani	end	mix	lan	lcd	isl	0	4	3	15	0.37	0.08
155	Neo	12	mix	1	1	1389.92	her	ani	mix	mix	top	ele	isl	0	4	3	19	0.76	0.06
155	Neo	12	mix	1	1	1389.92	her	ani	mix	mix	lan	lcd	isl	0	4	3	19	0.89	0.06
155	Neo	12	mix	1	1	1389.92	inv	ani	ect	her	top	ele	isl	0	4	3	19	0.85	0.06
155	Neo	12	mix	1	1	1389.92	inv	ani	ect	her	lan	lcd	isl	0	4	3	19	1.04	0.06
156	Aus	12	mix	1	0	805.99	pla	mix	pla	aut	top	ele	pol	0	4	3	56	0.83	0.02
157	Neo	10	for	0	1	1423.92	bir	ani	end	mix	top	ele	pol	0	3	2	32	0.08	0.03
157	Neo	10	for	0	1	1423.92	bir	ani	end	mix	top	pro	pol	0	3	2	32	0.87	0.03
157	Neo	10	for	0	1	1423.92	bir	ani	end	mix	veg	pla	pol	0	3	2	32	0.61	0.03
158	Nea	2	mix	0	0	1568.90	mam	ani	end	omn	veg	vec	plo	1	1	1	15	0.52	0.08

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
158	Nea	2	mix	0	0	1568.90	mam	ani	end	omn	veg	vec	plo	1	1	1	15	0.40	0.08
158	Nea	2	mix	0	0	1568.90	mam	ani	end	omn	soi	sov	plo	1	1	1	15	0.08	0.08
159	Nea	12	mon	0	0	938.13	mam	ani	end	mix	lan	lcd	pol	0	4	3	22	1.16	0.05
159	Nea	12	mon	0	0	938.13	mam	ani	end	mix	lan	lcd	pol	0	4	3	22	1.00	0.05
159	Nea	12	mon	0	0	1074.57	mam	ani	end	mix	lan	lcd	pol	0	4	3	16	0.69	0.08
159	Nea	12	mon	0	0	1074.57	mam	ani	end	mix	lan	lcd	pol	0	4	3	16	0.62	0.08
159	Nea	12	mon	0	0	1167.23	mam	ani	end	mix	lan	lcd	pol	0	4	3	18	0.64	0.07
159	Nea	12	mon	0	0	1167.23	mam	ani	end	mix	lan	lcd	pol	0	4	3	18	0.54	0.07
160	Pal	5	agr	0	0	725.42	inv	ani	ect	car	lan	lcp	pol	1	3	2	12	0.74	0.11
160	Pal	5	agr	0	0	725.42	inv	ani	ect	car	lan	lcp	pol	1	3	2	12	0.51	0.11
160	Pal	5	agr	0	0	725.42	inv	ani	ect	car	lan	lcp	pol	1	3	2	12	0.55	0.11
160	Pal	5	agr	0	0	725.42	inv	ani	ect	car	lan	lcp	pol	1	3	2	12	0.47	0.11
160	Pal	5	agr	0	0	725.42	inv	ani	ect	car	lan	lcp	pol	1	3	2	12	0.31	0.11
161	Pal	5	for	0	0	862.90	inv	ani	ect	car	veg	vec	plo	1	1	1	6	-0.73	0.33
161	Pal	5	for	0	0	862.90	inv	ani	ect	car	veg	pla	plo	1	1	1	6	0.04	0.33
161	Pal	5	for	0	0	862.90	inv	ani	ect	omn	veg	vec	plo	1	1	1	6	0.68	0.33
161	Pal	5	for	0	0	862.90	inv	ani	ect	omn	veg	pla	plo	1	1	1	6	0.20	0.33
162	Nea	12	xer	0	0	1175.80	inv	ani	ect	her	lan	lcd	pol	0	3	3	33	0.36	0.03
162	Nea	12	xer	0	0	1175.80	bir	ani	end	mix	lan	lcd	pol	0	3	3	16	0.94	0.08
162	Nea	12	xer	0	0	1139.12	inv	ani	ect	her	lan	lcd	plo	0	2	1	39	0.51	0.03
162	Nea	12	xer	0	0	1139.12	bir	ani	end	mix	lan	lcd	plo	0	2	1	25	0.14	0.05
162	Nea	12	xer	0	0	1230.38	inv	ani	ect	her	lan	lcd	plo	0	2	2	102	0.00	0.01
162	Nea	12	xer	0	0	1230.38	bir	ani	end	mix	lan	lcd	plo	0	2	2	32	0.10	0.03
162	Nea	12	xer	0	0	1120.17	inv	ani	ect	her	lan	lcd	plo	0	2	2	54	0.14	0.02
162	Nea	12	xer	0	0	1120.17	bir	ani	end	mix	lan	lcd	plo	0	2	2	28	0.00	0.04
162	Nea	12	xer	0	0	1175.80	inv	ani	ect	her	lan	lcd	plo	0	2	3	195	0.00	0.01
162	Nea	12	xer	0	0	1175.80	bir	ani	end	mix	lan	lcd	plo	0	2	3	84	0.00	0.01
163	Pal	3	mix	1	0	1054.96	inv	ani	ect	det	mix	mix	isl	0	3	3	43	2.10	0.02
163	Pal	3	mix	1	0	1054.96	inv	ani	ect	det	mix	mix	isl	0	4	3	23	1.24	0.05
163	Pal	3	mix	1	0	1054.96	inv	ani	ect	det	mix	mix	isl	0	3	3	20	1.36	0.06
164	Aus	12	mix	0	0	1723.30	mam	ani	end	mix	lan	lcd	gri	0	4	4	40	1.14	0.03
165	Pal	3	for	0	0	1055.03	inv	ani	ect	det	lan	lcd	pol	1	2	1	5	1.66	0.50
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.47	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.57	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.48	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.46	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.28	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.59	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.53	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.69	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	lan	lcd	plo	1	3	2	42	0.54	0.03
167	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	top	ele	plo	1	3	2	42	0.77	0.03
166	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	veg	vec	plo	1	3	2	42	1.09	0.03
166	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	veg	vec	plo	1	3	2	42	1.01	0.03

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
166	Nea	12	xer	0	0	1529.35	bir	ani	end	mix	veg	vec	plo	1	3	2	42	0.63	0.03
168	Pal	5	agr	0	0	725.42	inv	ani	ect	mix	lan	lcp	pol	1	2	2	15	0.79	0.08
168	Pal	5	agr	0	0	725.42	inv	ani	ect	mix	lan	lcp	pol	1	2	2	15	0.52	0.08
168	Pal	5	agr	0	0	725.42	inv	ani	ect	mix	lan	lcd	pol	1	2	2	15	0.30	0.08
168	Pal	5	agr	0	0	725.42	inv	ani	ect	mix	lan	lcp	pol	1	2	2	15	0.74	0.08
168	Pal	5	agr	0	0	725.42	inv	ani	ect	mix	lan	lcp	pol	1	3	2	15	0.50	0.08
168	Pal	5	agr	0	0	725.42	inv	ani	ect	mix	lan	lcp	pol	1	3	2	15	0.83	0.08
168	Pal	5	agr	0	0	725.42	inv	ani	ect	mix	lan	lcp	pol	1	3	2	15	0.47	0.08
169	Nea	2	xer	0	0	1749.35	pla	shr	pla	aut	soi	sod	pol	0	3	2	22	0.74	0.05
170	Nea	5	gra	0	0	1006.93	inv	ani	ect	her	lan	lcp	plo	0	2	1	17	0.55	0.07
171	mix	12	mix	0	0	1000.82	mam	ani	end	mix	top	ele	gri	1	4	4	3668	0.41	0.00
171	mix	12	mix	0	0	1000.82	mam	ani	end	mix	lan	lcd	gri	1	4	4	3668	0.14	0.00
171	mix	12	mix	0	0	1000.82	mam	ani	end	mix	top	ele	gri	1	4	4	3668	0.14	0.00
171	mix	12	mix	0	0	1000.82	mam	ani	end	mix	lan	lcd	gri	1	4	4	3668	0.14	0.00
172	Pal	12	for	0	0	904.95	pla	mix	pla	aut	veg	ved	plo	1	1	2	40	0.34	0.03
172	Pal	12	for	0	0	904.95	pla	mix	pla	aut	veg	ved	plo	1	1	2	40	0.63	0.03
172	Pal	12	for	0	0	904.95	pla	mix	pla	aut	veg	vec	plo	1	1	2	40	0.54	0.03
172	Pal	12	for	0	0	904.95	pla	mix	pla	aut	veg	ved	plo	1	1	2	40	0.27	0.03
172	Pal	12	for	0	0	904.95	pla	mix	pla	aut	veg	vec	plo	1	1	2	40	0.30	0.03
172	Pal	12	for	0	0	904.95	pla	mix	pla	aut	veg	vec	plo	1	1	2	40	-0.60	0.03
172	Pal	12	for	0	0	904.95	inv	ani	ect	car	veg	ved	plo	1	1	2	40	0.33	0.03
172	Pal	12	for	0	0	904.95	inv	ani	ect	car	veg	ved	plo	1	1	2	40	0.68	0.03
172	Pal	12	for	0	0	904.95	inv	ani	ect	car	veg	vec	plo	1	1	2	40	0.62	0.03
172	Pal	12	for	0	0	904.95	inv	ani	ect	car	veg	ved	plo	1	1	2	40	0.13	0.03
172	Pal	12	for	0	0	904.95	inv	ani	ect	car	veg	vec	plo	1	1	2	40	0.76	0.03
172	Pal	12	for	0	0	904.95	inv	ani	ect	car	veg	vec	plo	1	1	2	40	-0.42	0.03
173	Afr	12	mix	0	1	1374.54	inv	ani	ect	mix	veg	vec	plo	1	1	2	42	-0.47	0.03
174	Neo	10	for	0	1	1818.23	bir	ani	end	mix	veg	vec	pol	0	1	1	7	1.70	0.25
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	1.42	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	2.30	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	1.16	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	1.47	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	1.07	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	1.59	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	0.97	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	1.05	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	1.47	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	1.83	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	1.13	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	1.53	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	1.38	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	top	ele	plo	0	4	1	11	1.42	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	1.10	0.12
175	Nea	7	mix	0	0	884.91	bir	ani	end	mix	veg	pla	plo	0	4	1	11	1.33	0.12

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
176	Pal	3	mix	1	0	884.41	inv	ani	ect	mix	lan	lcd	isl	0	3	1	12	1.60	0.11
176	Pal	3	mix	1	0	884.41	inv	ani	ect	mix	lan	lcd	isl	0	3	1	12	1.15	0.11
177	Pal	3	mix	1	0	974.75	inv	ani	ect	det	top	ele	isl	0	3	2	13	2.11	0.10
177	Pal	3	mix	1	0	1108.94	inv	ani	ect	det	top	ele	isl	0	3	2	12	1.12	0.11
177	Pal	3	mix	1	0	974.75	inv	ani	ect	det	lan	lcd	isl	0	3	2	13	1.71	0.10
177	Pal	3	mix	1	0	1108.94	inv	ani	ect	det	lan	lcd	isl	0	3	2	12	1.57	0.11
178	Afr	12	mix	0	0	1548.73	bir	ani	end	mix	lan	lcd	gri	0	4	4	1858	0.33	0.00
178	Afr	12	mix	0	0	1548.73	bir	ani	end	mix	lan	lcd	gri	0	4	4	1858	0.04	0.00
178	Afr	12	mix	0	0	1548.73	bir	ani	end	mix	lan	lcd	gri	0	4	4	458	0.46	0.00
178	Afr	12	mix	0	0	1548.73	bir	ani	end	mix	lan	lcd	gri	0	4	4	458	0.10	0.00
178	Afr	12	mix	0	0	1548.73	bir	ani	end	mix	lan	lcd	gri	1	4	4	102	0.87	0.01
178	Afr	12	mix	0	0	1548.73	bir	ani	end	mix	lan	lcd	gri	1	4	4	102	0.22	0.01
180	Pal	6	mix	1	0	550.09	inv	ani	ect	car	lan	lcp	plo	1	2	1	6	-1.46	0.33
180	Pal	6	mix	1	0	550.09	inv	ani	ect	car	veg	pla	plo	1	2	1	6	0.61	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	lan	lcp	plo	1	2	1	6	-0.23	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	lan	lcd	plo	1	2	1	6	1.13	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	lan	pat	plo	1	2	1	6	0.83	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	veg	pla	plo	1	2	1	6	2.23	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	veg	pla	plo	1	2	1	6	1.20	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	lan	lcp	plo	1	2	1	6	-0.47	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	lan	lcd	plo	1	2	1	6	1.13	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	lan	pat	plo	1	2	1	6	1.07	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	veg	pla	plo	1	2	1	6	1.59	0.33
179	Pal	6	mix	1	0	550.09	inv	ani	ect	det	veg	pla	plo	1	2	1	6	1.28	0.33
181	Pal	5	mix	0	0	759.05	pla	her	pla	aut	lan	lcp	gri	1	3	2	87	0.89	0.01
181	Pal	5	mix	0	0	759.05	pla	her	pla	aut	lan	lcp	gri	1	3	2	87	0.50	0.01
182	Neo	2	mix	1	1	1304.57	pla	mix	pla	aut	top	ele	isl	0	4	3	18	1.19	0.07
183	Pal	5	agr	0	0	575.40	inv	ani	ect	her	lan	lcd	pol	0	3	2	16	0.58	0.08
183	Pal	5	agr	0	0	575.40	pla	mix	pla	aut	lan	lcd	pol	0	3	2	16	0.51	0.08
183	Pal	5	agr	0	0	575.40	inv	ani	ect	car	lan	lcd	pol	0	3	2	16	0.66	0.08
184	Pal	4	mix	1	0	968.31	inv	ani	ect	mix	top	ele	isl	0	4	3	65	1.26	0.02
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	top	ele	pol	0	3	2	10	1.06	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	top	ele	pol	0	3	2	10	0.85	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	lan	lcd	pol	0	3	2	10	1.17	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	top	ele	pol	0	3	2	10	0.77	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	top	ele	pol	0	3	2	10	1.21	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	lan	lcd	pol	0	3	2	10	0.79	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	lan	lcd	pol	0	3	2	10	0.76	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	top	ele	pol	0	3	2	10	0.80	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	top	ele	pol	0	3	2	10	1.34	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	lan	lcd	pol	0	3	2	10	0.87	0.14
185	Nea	5	mon	0	0	1103.79	pla	mix	pla	aut	top	ele	pol	0	3	2	10	0.95	0.14
186	Oce	12	mix	1	0	703.05	inv	ani	ect	mix	top	ele	isl	0	4	3	7	0.44	0.25
186	Oce	12	mix	1	0	703.05	inv	ani	ect	mix	veg	pla	isl	0	4	3	7	1.71	0.25

Table B.8 continued

ref	realm	biome	habitat	island	tropical	PET	taxon	growth	thermo	trophic	EH	EH-cat	unit	EA	grain	extent	n	ES	var
186	Oce	12	mix	1	0	703.05	inv	ani	ect	her	veg	pla	isl	0	4	3	7	2.44	0.25
186	Oce	12	mix	1	0	703.05	inv	ani	ect	mix	veg	pla	isl	0	4	3	7	0.70	0.25
186	Oce	12	mix	1	0	703.05	inv	ani	ect	mix	veg	pla	isl	0	4	3	7	2.03	0.25
186	Oce	12	mix	1	0	703.05	pla	mix	pla	aut	top	ele	isl	0	4	3	7	0.35	0.25
186	Oce	12	mix	1	0	703.05	inv	ani	ect	her	top	ele	isl	0	4	3	7	0.19	0.25
186	Oce	12	mix	1	0	703.05	inv	ani	ect	mix	top	ele	isl	0	4	3	7	0.88	0.25
186	Oce	12	mix	1	0	703.05	inv	ani	ect	mix	top	ele	isl	0	4	3	7	0.19	0.25
187	Aus	10	for	0	1	1509.16	mam	ani	end	mix	veg	vec	plo	1	2	1	8	-1.12	0.20
187	Aus	10	for	0	1	1509.16	mam	ani	end	mix	veg	vec	plo	1	2	1	8	1.56	0.20
188	Nea	5	mix	0	0	1068.55	bir	ani	end	mix	veg	vec	plo	0	2	1	21	0.78	0.06
189	Pal	12	mix	0	0	630.28	pla	mix	pla	aut	cli	cli	pol	0	3	3	350	0.66	0.00
189	Pal	12	mix	0	0	630.28	pla	mix	pla	aut	soi	sod	pol	0	3	3	350	0.34	0.00
190	Afr	3	for	0	0	1334.97	inv	ani	ect	her	veg	pla	tra	0	1	3	20	1.18	0.06
191	Pal	12	mix	0	0	997.77	pla	mix	pla	aut	lan	pat	pol	1	3	2	10	-0.05	0.14
191	Pal	12	mix	0	0	997.77	pla	mix	pla	aut	lan	lcd	pol	1	3	2	10	-0.88	0.14
192	mix	12	mix	0	0	909.89	pla	mix	pla	aut	top	ele	pol	0	4	4	178	0.57	0.01
192	mix	12	mix	0	0	909.89	pla	mix	pla	aut	top	ele	pol	0	4	4	165	0.55	0.01
192	mix	12	mix	0	0	909.89	pla	shr	pla	aut	top	ele	pol	0	4	4	170	0.63	0.01
192	mix	12	mix	0	0	909.89	pla	mix	pla	aut	top	ele	pol	0	4	4	175	0.55	0.01

B.6 Study characteristics

Table B.9 Summary of study characteristics. Overall, our meta-analysis included 192 studies and 1148 data points, which were assigned to different variables related to study location, taxon, and methodology. Categories for equal area, island, and tropical mean "no" (0) and "yes" (1). Numbers in parentheses give the number of studies/data points per variable level. Variables used in the statistical analysis are given in Table 3.2; note that spatial grain and extent were included in the analysis as continuous variables.

Variable	Details
equal area	0 (109/434); 1 (85/714)
spatial grain	$\leq$ 0.01 km^2 (40/151); $>$ 0.01 km^2 – 1 km^2 (54/254); $>$ 1 km^2 – 100 km^2 (49/391); $>$ 100 km^2 (63/352)
unit of analysis	grid cell (36/259); island (41/132); plot (58/334); polygon (56/406); transect (6/17)
spatial extent	$\leq$ 1,000 km^2 (57/235); $>$ 1,000 km^2 – 10,000 km^2 (45/327); $>$ 10,000 km^2 – 1,000,000 km^2 (61/424); $>$ 1,000,000 km^2 (32/160)
EH subject area	land cover (92/517); vegetation (68/315); climate (11/56); soil (16/37); topography (74/212); mixed (3/11)
EH measure category	land cover diversity (79/285); land cover proportion (19/108); patchiness (10/124); plant diversity (37/148); vegetation complexity (29/100); vegetation dimension (16/67); climate (11/56); soil diversity (10/25); soil variables (7/12); elevation diversity (67/178); microtopography (5/5); profile (7/29); mixed (3/11)
EH data source	database (5/96); field data (68/310); GIS data (29/305); literature data (36/144); maps (36/131); remote sensing data (25/88); various (e.g. literature, museum, and field data) (1/3); NA (19/71)
realm	Afrotropic (18/109); Australasia (11/66); Indo-Malay (3/10); Nearctic (35/307); Neotropic (34/221); Oceania (4/13); Palearctic (80/380); mixed (11/42)
biome	boreal forests/ taiga (4/35); deserts and xeric shrublands (7/15); Mediterranean forests, woodlands, and scrub (24/99); montane grasslands and shrublands (2/2); temperate broadleaf and mixed forests (46/226); temperate coniferous forests (5/16); temperate grasslands, savannas, and shrublands (4/24); tropical and subtropical dry broadleaf forests (4/65); tropical and subtropical grasslands, savannas, and shrublands (9/36); tropical and subtropical moist broadleaf forests (18/61); tundra (1/2); various (73/567)
habitat type	forest (57/367); non-forest (46/306); mixed (91/475)
fine habitat type	agricultural (18/185); forest (57/367); grassland (16/57); montane (3/23); xeric (9/41); mixed (91/475)
island	0 (142/956); 1 (52/192)
tropical	0 (142/847); 1 (51/301)
broad taxon	plants (67/336); invertebrates (56/289); vertebrates (85/523)
fine taxon	plants (67/336); invertebrates (56/289); birds (54/284); herptiles (13/36); mammals (29/109); mixed vertebrates (3/94)
taxon data source	database (9/60); field data (117/742); GIS data (1/1); herbarium data (1/1); literature data (60/324); various (e.g. literature, museum, and field data) (4/19); NA (1/1)
growth form	animal (135/812); herbs (15/87); shrubs or trees (16/46); mixed plants (46/203)
thermoregulation	ectotherm (67/323); endotherm (78/393); mixed (4/96); plant (67/336)
trophic group	autotroph (67/336); carnivore (17/51); detritivore (4/18); frugivore (6/38); herbivore (26/154); insectivore (3/8); omnivore (7/15); mixed (95/528)

B.7 Partial relationships between spatial scale and effect size

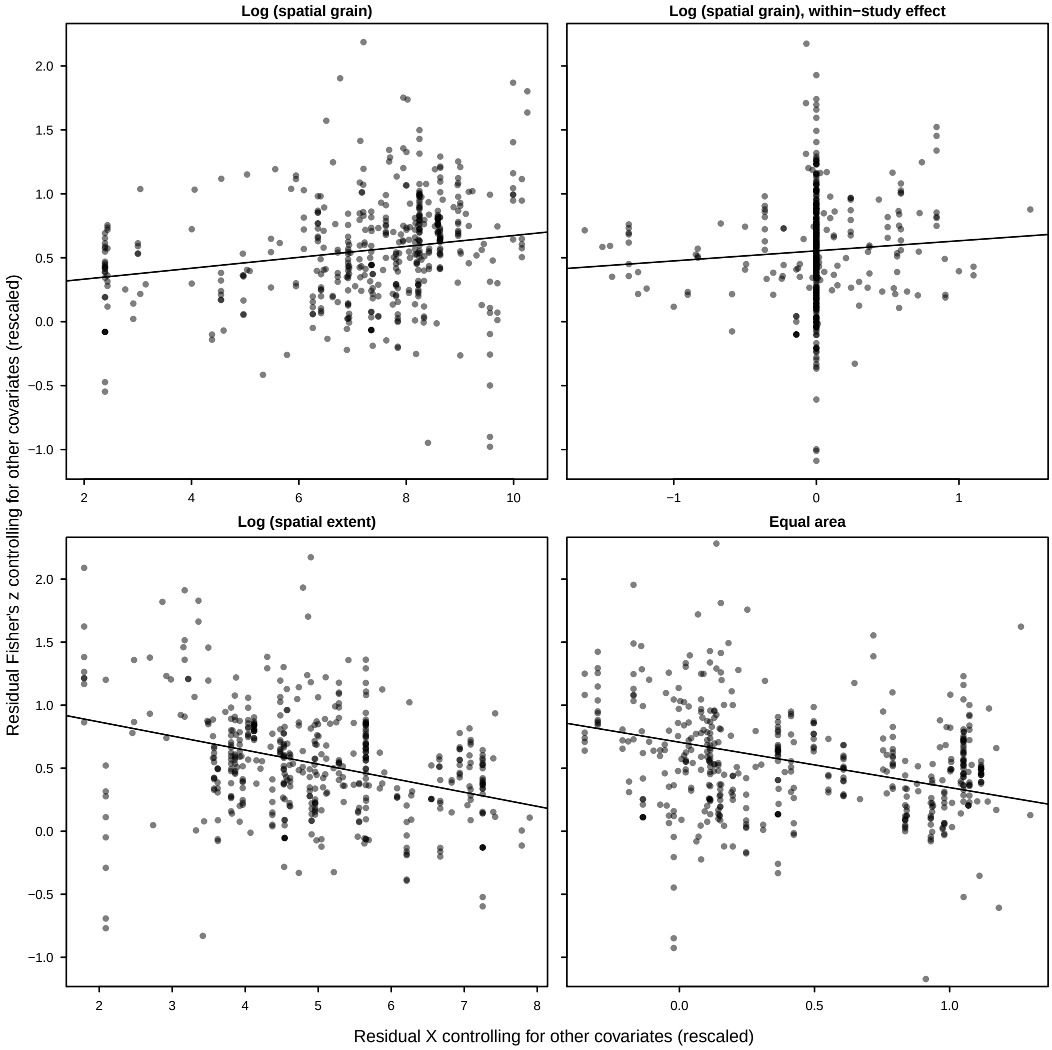


Figure B.1 Partial regression plots showing the relationship between different spatial scale variables and EH–richness relationships for subgroup I (considering only the EH measure categories elevation and land cover diversity) while accounting for the other covariates in the multi-predictor meta-regression (full model 3, Table 3.3a). The residuals on the y-axis are derived from a meta-regression of the effect size, Fisher's *z*, against all covariates of model 3 except for the x-variable of interest (i.e. between-study effects for spatial grain, spatial extent, and equal area, and within-study effects for spatial grain; compare Table 3.3a). The residuals on the x-axis come from a meta-regression of the x-variable of interest against all other covariates of model 3. For details on covariates see Table 3.2. Plots are rescaled to the original range of raw variables by adding the means of the raw x- and y-variables to the residuals.

B.8 Additional meta-regressions

Table B.10 Mixed-effects meta-regression for subgroup I (EH measure categories elevation and land cover diversity; 125/418 studies/data points) including fine instead of broad taxonomic group (compare Table 3.3a). Data points analysing mixed vertebrate groups are excluded. Given are estimates of coefficients *b* for between-study effects (within-study effect for grain.centred), robust standard errors *SE*, and 99% confidence intervals *CI*. For details on covariates see Table 3.2; reference levels for categorical variables: EH measure category: *land cover diversity*; habitat: *forest*; taxon: *plants*. R^2: 0.10. Significance levels: *** 0.001, ** 0.01, * 0.05, · 0.1.

Subgroup I	b	SE	CI
intercept	.71**	.21	± .56
equal area	−.38***	.09	± .23
grain	.05*	.02	± .05
grain.centred	.07*	.04	± .09
extent	−.12***	.03	± .08
elevation diversity	−.02	.11	± .30
habitat mixed	.35**	.11	± .30
habitat non-forest	.11	.13	± .33
PET	.00	.00	± .00
invertebrates	−.07	.12	± .32
birds	−.03	.10	± .25
herptiles	−.30·	.17	± .45
mammals	.07	.12	± .32

Table B.11 Mixed-effects meta-regression for subgroup II (EH measure categories vegetation complexity and plant diversity; 60/238 studies/data points) including fine instead of broad taxonomic group (compare Table 3.3b). Data points analysing mixed vertebrate groups are excluded. Given are estimates of coefficients *b* for between-study effects, robust standard errors *SE*, and 99% confidence intervals *CI*. For details on covariates see Table 3.2; reference levels for categorical variables: EH measure category: *plant diversity*; habitat: *forest*; taxon: *birds*. R^2: 0 (negative, truncated to zero). Significance levels: * 0.05, · 0.1.

Subgroup II	b	SE	CI
intercept	.75*	.30	± .81
equal area	−.12	.13	± .36
grain	.06·	.03	± .08
extent	−.02	.05	± .12
vegetation complexity	−.22	.19	± .50
habitat mixed	−.05	.16	± .44
habitat non-forest	.17	.23	± .61
island	.15	.15	± .42
herptiles	−.04	.24	± .64
invertebrates	−.22	.18	± .49
mammals	.09	.20	± .54

B.9 Publication bias

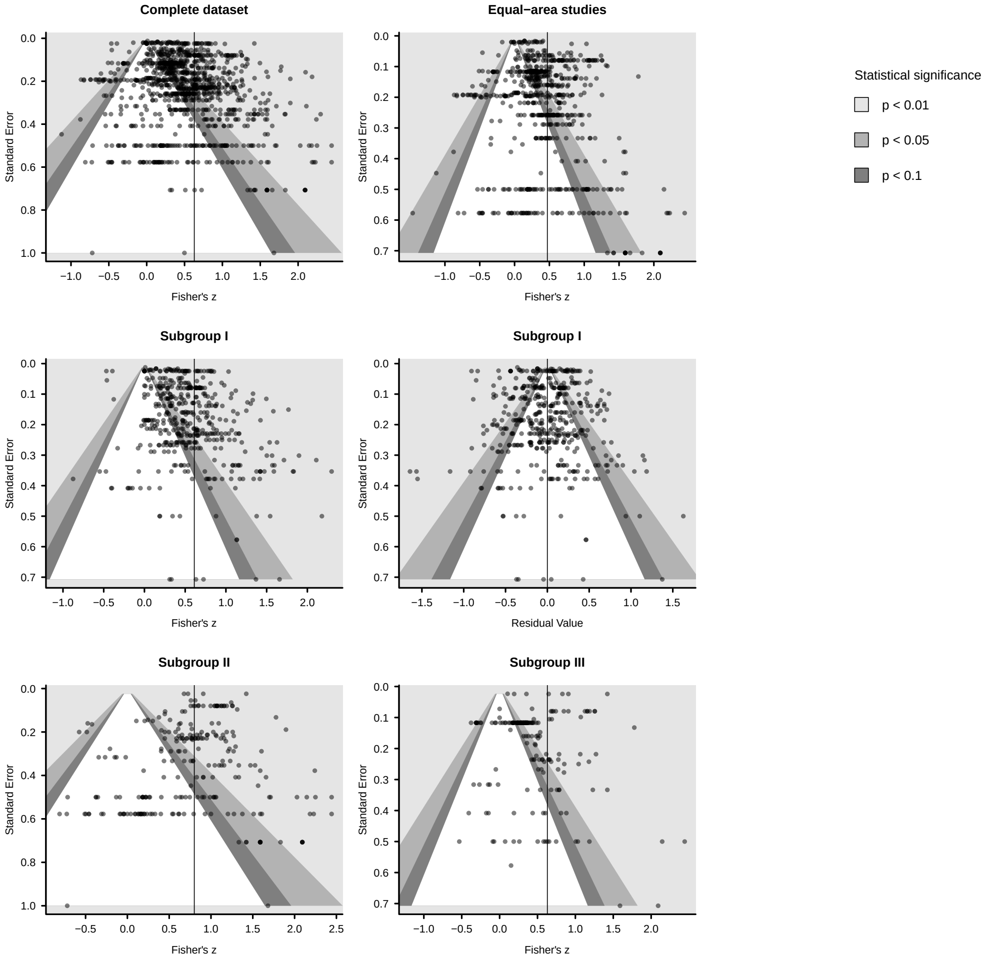


Figure B.2 Contour-enhanced funnel plots for the complete dataset, equal-area studies only, and subgroups I (EH measure categories elevation diversity and land cover diversity), II (EH measure categories vegetation complexity and plant diversity), and III (herbivores and EH subject areas land cover, topographic, and vegetation EH). Plots show standard errors against effect size estimates, i.e. Fisher's *z*, or against residuals of a mixed-effects model (model 3) for subgroup I. Vertical lines indicate weighted mean effect size estimates or zero for residual values. Shades of grey indicate areas of statistical significance of effect size estimates. When studies appear to be missing in areas of low statistical significance, funnel plot asymmetry is more likely to be caused by publication bias, whereas it is more likely to caused by other factors, such as heterogeneity or study quality, for gaps in areas of higher statistical significance.

Table B.12 Egger's regression tests for the complete dataset and subgroups of the data as in Figure B.2. Estimates b are slopes of weighted regressions of effect size estimates on their standard errors. For the mixed-effects model (MEM), the estimate is the intercept of a regression test using residuals of the full model 3 of subgroup I. Funnel plot asymmetry is indicated if estimates are significantly different from zero ($p < 0.05$).

	b	t	p
complete dataset	0.84	3.41	0.00
equal-area studies	0.47	1.30	0.20
subgroup I	1.48	4.05	0.00
subgroup I (MEM)	0.25	0.79	0.43
subgroup II	0.15	0.34	0.73
subgroup III	0.31	0.46	0.65

C

Supporting information to chapter 4

C.1 Spatial autocorrelation in model residuals

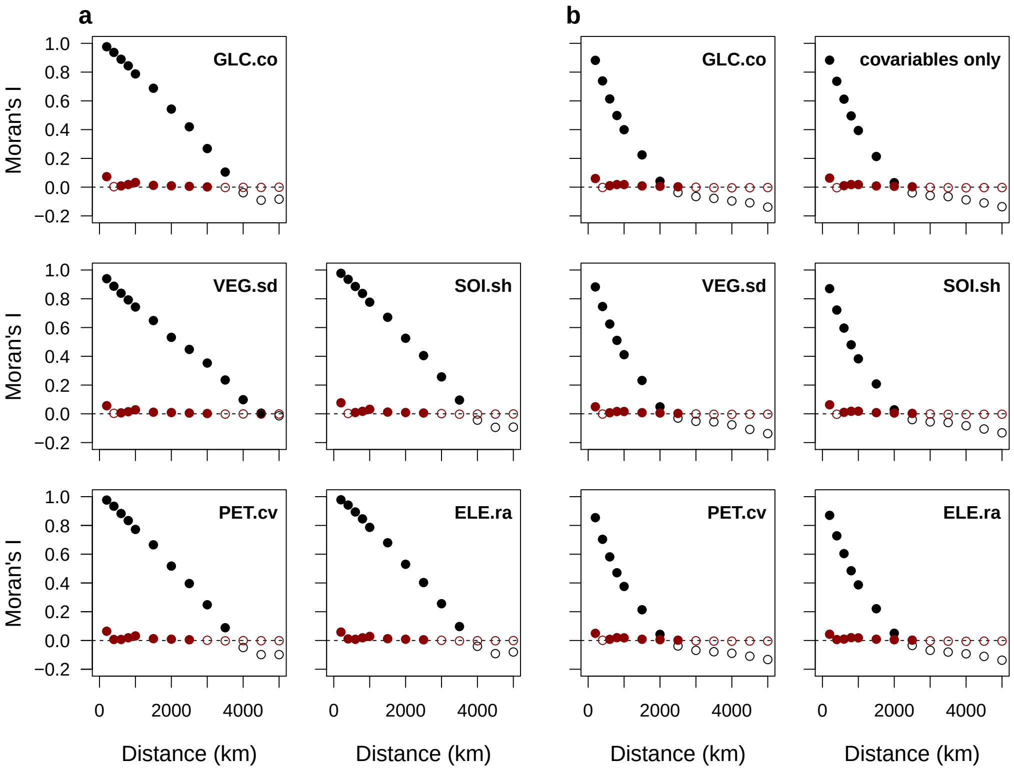


Figure C.1 Correlograms for residuals from ordinary least squares (OLS; black dots) and simultaneous autoregressive (SAR; red dots) models at 111 km × 111 km grain. One exemplary correlogram per EH subject area is given for (a) single-predictor models and (b) multi-predictor models including one EH measure each as indicated by the legend. Multi-predictor models included mean actual evapotranspiration, annual mean temperature, biogeographic region, and human influence index alone (*covariables only*) or in addition to one particular EH measure. Filled dots indicate Moran's I values that are significantly different from zero at $p = 0.5$. Abbreviated EH measure names are GLC.co, number of land cover classes; VEG.sd, standard deviation of canopy height; PET.cv, coefficient of variation of potential evapotranspiration; SOI.sh, Shannon entropy of major soil groups; ELE.ra, elevation range.

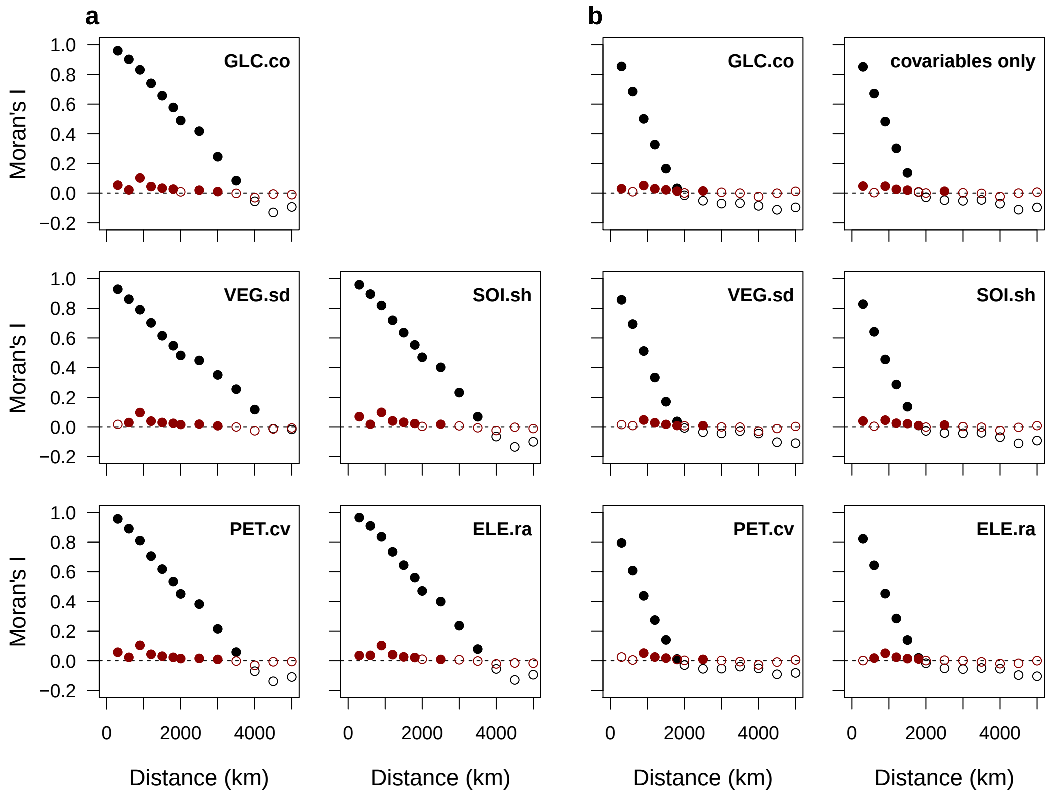


Figure C.2 Correlograms for residuals from ordinary least squares (OLS; black dots) and simultaneous autoregressive (SAR; red dots) models at 222 km × 222 km grain. One exemplary correlogram per EH subject area is given for (a) single-predictor models and (b) multi-predictor models including one EH measure each as indicated by the legend. Multi-predictor models included mean actual evapotranspiration, annual mean temperature, biogeographic region, and human influence index alone (*covariables only*) or in addition to one particular EH measure. Filled dots indicate Moran's I values that are significantly different from zero at $p = 0.5$. Abbreviated EH measure names are GLC.co, number of land cover classes; VEG.sd, standard deviation of canopy height; PET.cv, coefficient of variation of potential evapotranspiration; SOI.sh, Shannon entropy of major soil groups; ELE.ra, elevation range.

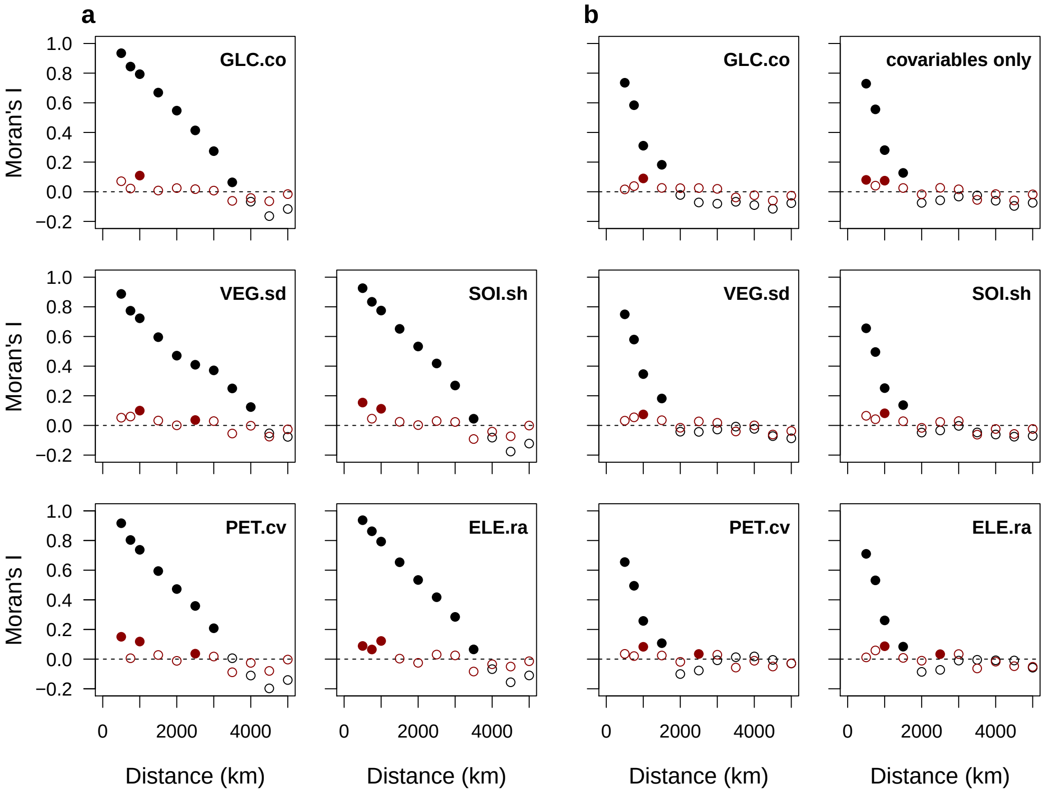


Figure C.3 Correlograms for residuals from ordinary least squares (OLS; black dots) and simultaneous autoregressive (SAR; red dots) models at 444 km × 444 km grain. One exemplary correlogram per EH subject area is given for (a) single-predictor models and (b) multi-predictor models including one EH measure each as indicated by the legend. Multi-predictor models included mean actual evapotranspiration, annual mean temperature, biogeographic region, and human influence index alone (*covariables only*) or in addition to one particular EH measure. Filled dots indicate Moran's I values that are significantly different from zero at $p = 0.5$. Abbreviated EH measure names are GLC.co, number of land cover classes; VEG.sd, standard deviation of canopy height; PET.cv, coefficient of variation of potential evapotranspiration; SOI.sh, Shannon entropy of major soil groups; ELE.ra, elevation range.

C.2 Collinearity among EH measures

Table C.1 Spearman rank correlation coefficients between 51 EH measures at 111 km × 111 km grain. Diagonal is marked in bold. Abbreviated measure names consist of three letters for each variable and two letters for calculation methods, e.g. ELE.sd, standard deviation of elevation. Variables: ELE, elevation; GLC, land cover classes; NPP, annual net primary production; PET, mean annual potential evapotranspiration; PLA, vascular plant species richness; PRE, annual precipitation; SOI, major soil groups; TEM, annual mean temperature; VEG, canopy height. Calculation methods: co, count; cv, coefficient of variation; ma, maximum; me, mean; ra, range; sd, standard deviation; sh, Shannon entropy; si, Simpson index; tr, terrain ruggedness index.

	GLC.co	GLC.sh	GLC.si	NPP.co	NPP.cv	NPP.ra	NPP.sd	NPP.sh	NPP.si	NPP.tr	PLA.co	VEG.co	VEG.cv	VEG.ma	VEG.me	VEG.ra	VEG.sd	VEG.sh	VEG.si	VEG.tr	PET.co	PET.cv	PET.ra	PET.sd	PET.sh
GLC.co	**1.00**	.69	.60	.48	-.02	.46	.50	.52	.51	.17	.20	.48	-.05	.49	.54	.49	.56	.56	.55	.51	.05	.36	.05	.06	.05
GLC.sh	.69	**1.00**	.98	.47	.10	.45	.57	.61	.61	.29	.18	.45	.11	.41	.40	.42	.61	.51	.49	.60	.18	.40	.18	.19	.19
GLC.si	.60	.98	**1.00**	.44	.10	.42	.54	.58	.58	.29	.18	.42	.15	.38	.36	.38	.58	.48	.46	.58	.19	.38	.19	.20	.20
NPP.co	.48	.47	.44	**1.00**	-.20	.99	.90	.85	.82	.10	.72	.82	-.15	.80	.72	.81	.77	.77	.72	.73	.25	.23	.25	.23	.22
NPP.cv	-.02	.10	.10	-.20	**1.00**	-.22	.06	.03	.04	.70	-.21	-.19	.36	-.22	-.35	-.21	-.10	-.26	-.28	-.12	.33	.35	.33	.33	.33
NPP.ra	.46	.45	.42	.99	-.22	**1.00**	.88	.84	.80	.08	.73	.82	-.16	.81	.73	.81	.76	.77	.72	.73	.24	.21	.24	.22	.21
NPP.sd	.50	.57	.54	.90	.06	.88	**1.00**	.94	.91	.35	.61	.76	-.07	.73	.64	.73	.79	.73	.68	.74	.28	.33	.28	.27	.27
NPP.sh	.52	.61	.58	.85	.03	.84	.94	**1.00**	.99	.28	.54	.71	-.03	.67	.59	.68	.76	.69	.64	.75	.31	.38	.31	.31	.31
NPP.si	.51	.61	.58	.82	.04	.80	.91	.99	**1.00**	.28	.52	.68	-.02	.65	.57	.65	.74	.67	.62	.74	.31	.38	.31	.31	.30
NPP.tr	.17	.29	.29	.10	.70	.08	.35	.28	.28	**1.00**	.08	.10	.38	.06	-.06	.07	.18	.02	.00	.18	.30	.36	.30	.30	.30
PLA.co	.20	.18	.18	.72	-.21	.73	.61	.54	.52	.08	**1.00**	.71	-.03	.70	.53	.70	.55	.54	.49	.53	.28	.08	.28	.24	.23
VEG.co	.48	.45	.42	.82	-.19	.82	.76	.71	.68	.10	.71	**1.00**	-.16	.97	.80	.97	.84	.84	.77	.74	.31	.31	.31	.27	.26
VEG.cv	-.05	.11	.15	-.15	.36	-.16	-.07	-.03	-.02	.38	-.03	-.16	**1.00**	-.20	-.45	-.20	-.08	-.36	-.40	-.04	.22	.18	.22	.23	.23
VEG.ma	.49	.41	.38	.80	-.22	.81	.73	.67	.65	.06	.70	.97	-.20	**1.00**	.85	1.00	.83	.83	.76	.71	.28	.30	.28	.24	.23
VEG.me	.54	.40	.36	.72	-.35	.73	.64	.59	.57	-.06	.53	.80	-.45	.85	**1.00**	.84	.75	.92	.92	.66	.04	.17	.04	.02	.02
VEG.ra	.49	.42	.38	.81	-.21	.81	.73	.68	.65	.07	.70	.97	-.20	1.00	.84	**1.00**	.83	.83	.77	.71	.28	.31	.28	.24	.23
VEG.sd	.56	.61	.58	.77	-.10	.76	.79	.76	.74	.18	.55	.84	-.08	.83	.75	.83	**1.00**	.84	.77	.92	.28	.38	.28	.27	.26
VEG.sh	.56	.51	.48	.77	-.26	.77	.73	.69	.67	.02	.54	.84	-.36	.83	.92	.83	.84	**1.00**	.98	.77	.13	.23	.13	.11	.11
VEG.si	.55	.49	.46	.72	-.28	.72	.68	.64	.62	.00	.49	.77	-.40	.76	.92	.77	.77	.98	**1.00**	.72	.07	.18	.07	.05	.05
VEG.tr	.51	.60	.58	.73	-.12	.73	.74	.75	.74	.18	.53	.74	-.04	.71	.66	.71	.92	.77	.72	**1.00**	.27	.35	.27	.26	.26
PET.co	.05	.18	.19	.25	.33	.24	.28	.31	.31	.30	.28	.31	.22	.28	.04	.28	.28	.13	.07	.27	**1.00**	.78	1.00	.96	.95
PET.cv	.36	.40	.38	.23	.35	.21	.33	.38	.38	.36	.08	.31	.18	.30	.17	.31	.38	.23	.18	.35	.78	**1.00**	.78	.83	.83
PET.ra	.05	.18	.19	.25	.33	.24	.28	.31	.31	.30	.28	.31	.22	.28	.04	.28	.28	.13	.07	.27	1.00	.78	**1.00**	.96	.95
PET.sd	.06	.19	.20	.23	.33	.22	.27	.31	.31	.30	.24	.27	.23	.24	.02	.24	.27	.11	.05	.26	.96	.83	.96	**1.00**	1.00
PET.sh	.05	.19	.20	.22	.33	.21	.27	.31	.30	.30	.23	.26	.23	.23	.02	.23	.26	.11	.05	.26	.95	.83	.95	1.00	**1.00**
PET.si	.05	.18	.19	.21	.33	.20	.26	.30	.30	.29	.22	.25	.22	.22	.01	.22	.25	.10	.05	.25	.93	.83	.93	.99	1.00
PET.tr	.13	.21	.21	.34	.19	.34	.33	.35	.34	.21	.36	.45	.06	.45	.25	.45	.41	.29	.22	.39	.85	.66	.85	.78	.78
PRE.co	.29	.34	.34	.69	-.04	.69	.66	.64	.63	.21	.67	.70	.03	.68	.54	.68	.63	.56	.51	.58	.52	.34	.52	.46	.45
PRE.cv	-.17	-.07	-.06	-.18	.43	-.20	-.12	-.09	-.09	.21	-.12	-.14	.21	-.17	-.36	-.17	-.14	-.29	-.33	-.17	.55	.39	.55	.53	.52
PRE.ra	.26	.32	.32	.67	-.01	.67	.64	.62	.60	.22	.67	.68	.04	.66	.51	.66	.61	.53	.48	.55	.55	.36	.55	.49	.48
PRE.sd	.24	.31	.32	.66	-.02	.65	.63	.61	.59	.22	.65	.66	.04	.64	.50	.64	.59	.52	.47	.54	.49	.31	.49	.45	.44
PRE.sh	.27	.33	.33	.68	-.06	.68	.65	.63	.62	.20	.66	.68	.02	.65	.53	.66	.62	.56	.51	.57	.45	.29	.45	.41	.40
PRE.si	.27	.33	.33	.68	-.06	.67	.64	.63	.61	.20	.66	.67	.02	.65	.53	.65	.62	.56	.51	.57	.44	.28	.44	.40	.39
PRE.tr	.36	.40	.38	.69	-.03	.69	.66	.65	.63	.20	.60	.73	-.03	.73	.60	.73	.68	.62	.56	.63	.60	.51	.60	.55	.54
TEM.co	.24	.30	.29	.25	.33	.24	.30	.34	.33	.32	.20	.36	.18	.35	.15	.35	.36	.21	.15	.32	.88	.83	.88	.82	.81
TEM.cv	.28	.34	.32	.23	.35	.21	.30	.34	.34	.34	.13	.32	.18	.31	.14	.31	.35	.20	.15	.32	.82	.88	.82	.82	.81
TEM.ra	.24	.30	.29	.25	.33	.24	.30	.34	.33	.32	.20	.36	.18	.35	.15	.35	.36	.21	.15	.32	.88	.83	.88	.82	.81
TEM.sd	.26	.32	.31	.23	.35	.22	.30	.34	.33	.33	.15	.32	.18	.31	.13	.31	.35	.20	.14	.31	.84	.87	.84	.83	.82
TEM.sh	.26	.32	.31	.22	.35	.21	.29	.33	.33	.33	.13	.31	.18	.30	.13	.30	.34	.19	.14	.32	.82	.87	.82	.82	.82
TEM.si	.26	.32	.31	.21	.34	.20	.28	.32	.32	.33	.12	.29	.18	.28	.13	.29	.33	.19	.14	.31	.80	.87	.80	.81	.81
TEM.tr	.27	.31	.29	.36	.18	.36	.36	.38	.37	.21	.31	.49	.01	.50	.34	.51	.48	.36	.30	.43	.77	.72	.77	.71	.71
SOI.co	.24	.31	.29	.15	.15	.14	.19	.22	.22	.18	.04	.17	.14	.15	.11	.15	.24	.17	.15	.21	.25	.33	.25	.23	.22
SOI.sh	.25	.31	.30	.15	.14	.14	.19	.22	.22	.16	.03	.14	.12	.13	.10	.13	.22	.16	.14	.18	.22	.29	.22	.21	.20
SOI.si	.24	.29	.28	.14	.13	.13	.18	.20	.20	.15	.02	.13	.10	.11	.09	.11	.20	.14	.13	.16	.20	.26	.20	.20	.18
ELE.co	.20	.27	.26	.25	.31	.24	.28	.32	.31	.28	.22	.36	.16	.35	.15	.36	.35	.20	.15	.30	.87	.77	.87	.79	.78
ELE.cv	.30	.34	.32	.30	.22	.29	.34	.36	.35	.22	.18	.38	.09	.38	.24	.39	.41	.29	.23	.34	.72	.69	.72	.68	.66
ELE.ra	.20	.27	.26	.25	.30	.24	.28	.32	.31	.28	.22	.36	.15	.35	.15	.36	.35	.20	.15	.30	.87	.77	.87	.79	.78
ELE.sd	.20	.28	.27	.23	.31	.23	.27	.31	.30	.27	.19	.33	.16	.33	.14	.33	.34	.19	.14	.30	.84	.78	.84	.80	.78
ELE.sh	.19	.27	.26	.22	.30	.21	.25	.30	.29	.26	.17	.32	.15	.31	.13	.31	.33	.19	.14	.30	.83	.78	.83	.79	.78
ELE.si	.19	.26	.25	.21	.30	.20	.24	.29	.28	.25	.16	.30	.15	.30	.13	.30	.32	.18	.13	.29	.82	.77	.82	.78	.78
ELE.tr	.29	.32	.30	.37	.17	.37	.37	.40	.39	.21	.31	.50	.00	.52	.36	.52	.49	.38	.32	.44	.76	.72	.76	.70	.70

PET.si	PET.tr	PRE.co	PRE.cv	PRE.ra	PRE.sd	PRE.sh	PRE.si	PRE.tr	TEM.co	TEM.cv	TEM.ra	TEM.sd	TEM.sh	TEM.si	TEM.tr	SOI.co	SOI.sh	SOI.si	ELE.co	ELE.cv	ELE.ra	ELE.sd	ELE.sh	ELE.si	ELE.tr
.05	.13	.29	-.17	.26	.24	.27	.27	.36	.24	.28	.24	.26	.26	.26	.27	.24	.25	.24	.20	.30	.20	.20	.19	.19	.29
.18	.21	.34	-.07	.32	.31	.33	.33	.40	.30	.34	.30	.32	.32	.32	.31	.31	.31	.29	.27	.34	.27	.28	.27	.26	.32
.19	.21	.34	-.06	.32	.32	.33	.33	.38	.29	.32	.29	.31	.31	.31	.29	.29	.30	.28	.26	.32	.26	.27	.26	.25	.30
.21	.34	.69	-.18	.67	.66	.68	.68	.69	.25	.23	.25	.23	.22	.21	.36	.15	.15	.14	.25	.30	.25	.23	.22	.21	.37
.33	.19	-.04	.43	-.01	-.02	-.06	-.06	-.03	.33	.35	.33	.35	.35	.34	.18	.15	.14	.13	.31	.22	.30	.31	.30	.30	.17
.20	.34	.69	-.20	.67	.65	.68	.67	.69	.24	.21	.24	.22	.21	.20	.36	.14	.14	.13	.24	.29	.24	.23	.21	.20	.37
.26	.33	.66	-.12	.64	.63	.65	.64	.66	.30	.30	.30	.30	.29	.28	.36	.19	.19	.18	.28	.34	.28	.27	.25	.24	.37
.30	.35	.64	-.09	.62	.61	.63	.63	.65	.34	.34	.34	.34	.33	.32	.38	.22	.22	.20	.32	.36	.32	.31	.30	.29	.40
.30	.34	.63	-.09	.60	.59	.62	.61	.63	.33	.34	.33	.33	.33	.32	.37	.22	.22	.20	.31	.35	.31	.30	.29	.28	.39
.29	.21	.21	.21	.22	.22	.20	.20	.20	.32	.34	.32	.33	.33	.33	.21	.18	.16	.15	.28	.22	.28	.27	.26	.25	.21
.22	.36	.67	-.12	.67	.65	.66	.66	.60	.20	.13	.20	.15	.13	.12	.31	.04	.03	.02	.22	.18	.22	.19	.17	.16	.31
.25	.45	.70	-.14	.68	.66	.68	.67	.73	.36	.32	.36	.32	.31	.29	.49	.17	.14	.13	.36	.38	.36	.33	.32	.30	.50
.22	.06	.03	.21	.04	.04	.02	.02	-.03	.18	.18	.18	.18	.18	.18	.01	.14	.12	.10	.16	.09	.15	.16	.15	.15	.00
.22	.45	.68	-.17	.66	.64	.65	.65	.73	.35	.31	.35	.31	.30	.28	.50	.15	.13	.11	.35	.38	.35	.33	.31	.30	.52
.01	.25	.54	-.36	.51	.50	.53	.53	.60	.15	.14	.15	.13	.13	.13	.34	.11	.10	.09	.15	.24	.15	.14	.13	.13	.36
.22	.45	.68	-.17	.66	.64	.66	.65	.73	.35	.31	.35	.31	.30	.29	.51	.15	.13	.11	.36	.39	.36	.33	.31	.30	.52
.25	.41	.63	-.14	.61	.59	.62	.62	.68	.36	.35	.36	.35	.34	.33	.48	.24	.22	.20	.35	.41	.35	.34	.33	.32	.49
.10	.29	.56	-.29	.53	.52	.56	.56	.62	.21	.20	.21	.20	.19	.19	.36	.17	.16	.14	.20	.29	.20	.19	.19	.18	.38
.05	.22	.51	-.33	.48	.47	.51	.51	.56	.15	.15	.15	.14	.14	.14	.30	.15	.14	.13	.15	.23	.15	.14	.14	.13	.32
.25	.39	.58	-.17	.55	.54	.57	.57	.63	.32	.32	.32	.31	.32	.31	.43	.21	.18	.16	.30	.34	.30	.30	.30	.29	.44
.93	.85	.52	.55	.55	.49	.45	.44	.60	.88	.82	.88	.84	.82	.80	.77	.25	.22	.20	.87	.72	.87	.84	.83	.82	.76
.83	.66	.34	.39	.36	.31	.29	.28	.51	.83	.88	.83	.87	.87	.87	.72	.33	.29	.26	.77	.69	.77	.78	.78	.77	.72
.93	.85	.52	.55	.55	.49	.45	.44	.60	.88	.82	.88	.84	.82	.80	.77	.25	.22	.20	.87	.72	.87	.84	.83	.82	.76
.99	.78	.46	.53	.49	.45	.41	.40	.55	.82	.82	.82	.83	.82	.81	.71	.23	.21	.20	.79	.68	.79	.80	.79	.78	.70
1.00	.78	.45	.52	.48	.44	.40	.39	.54	.81	.81	.81	.82	.82	.81	.71	.22	.20	.18	.78	.66	.78	.78	.78	.78	.70
1.00	.75	.43	.51	.46	.42	.38	.38	.52	.78	.79	.78	.80	.81	.80	.69	.21	.19	.18	.75	.63	.75	.76	.76	.76	.67
.75	**1.00**	.58	.43	.61	.55	.52	.51	.77	.84	.78	.84	.79	.79	.77	.95	.20	.16	.15	.88	.74	.88	.87	.88	.87	.95
.43	.58	**1.00**	.27	.99	.97	.98	.97	.88	.47	.39	.47	.41	.39	.36	.54	.15	.15	.14	.50	.48	.50	.46	.44	.42	.54
.51	.43	.27	**1.00**	.32	.33	.26	.26	.20	.49	.45	.49	.46	.45	.44	.37	.11	.11	.10	.52	.43	.52	.51	.50	.49	.35
.46	.61	.99	.32	**1.00**	.98	.97	.96	.88	.50	.42	.50	.43	.41	.39	.57	.16	.15	.14	.53	.51	.53	.49	.47	.45	.56
.42	.55	.97	.33	.98	**1.00**	.99	.99	.83	.43	.36	.43	.38	.36	.34	.50	.13	.13	.12	.46	.45	.46	.43	.41	.39	.50
.38	.52	.98	.26	.97	.99	**1.00**	1.00	.83	.40	.34	.40	.35	.33	.31	.48	.12	.13	.12	.43	.43	.43	.39	.38	.36	.48
.38	.51	.97	.26	.96	.99	1.00	**1.00**	.82	.39	.33	.39	.34	.32	.30	.47	.12	.13	.12	.42	.42	.42	.39	.37	.35	.47
.52	.77	.88	.20	.88	.83	.83	.82	**1.00**	.63	.57	.63	.58	.57	.55	.78	.21	.18	.16	.65	.62	.65	.63	.62	.61	.78
.78	.84	.47	.49	.50	.43	.40	.39	.63	**1.00**	.95	1.00	.96	.95	.92	.86	.31	.27	.24	.96	.83	.96	.93	.91	.90	.85
.79	.78	.39	.45	.42	.36	.34	.33	.57	.95	**1.00**	.95	1.00	.99	.98	.82	.30	.27	.25	.88	.81	.88	.90	.90	.89	.82
.78	.84	.47	.49	.50	.43	.40	.39	.63	1.00	.95	**1.00**	.96	.95	.92	.86	.31	.27	.24	.96	.83	.96	.93	.91	.90	.85
.80	.79	.41	.46	.43	.38	.35	.34	.58	.96	1.00	.96	**1.00**	.99	.98	.82	.30	.27	.25	.89	.81	.89	.91	.90	.89	.82
.81	.79	.39	.45	.41	.36	.33	.32	.57	.95	.99	.95	.99	**1.00**	1.00	.82	.29	.26	.23	.87	.79	.87	.90	.90	.90	.82
.80	.77	.36	.44	.39	.34	.31	.30	.55	.92	.98	.92	.98	1.00	**1.00**	.81	.28	.25	.23	.85	.77	.85	.88	.89	.89	.80
.69	.95	.54	.37	.57	.50	.48	.47	.78	.86	.82	.86	.82	.82	.81	**1.00**	.25	.20	.18	.89	.79	.89	.89	.89	.89	1.00
.21	.20	.15	.11	.16	.13	.12	.12	.21	.31	.30	.31	.30	.29	.28	.25	**1.00**	.81	.71	.28	.29	.28	.27	.26	.26	.24
.19	.16	.15	.11	.15	.13	.13	.13	.18	.27	.27	.27	.27	.26	.25	.20	.81	**1.00**	.98	.24	.29	.24	.24	.22	.22	.19
.18	.15	.14	.10	.14	.12	.12	.12	.16	.24	.25	.24	.25	.23	.23	.18	.71	.98	**1.00**	.22	.27	.22	.22	.20	.19	.17
.75	.88	.50	.52	.53	.46	.43	.42	.65	.96	.88	.96	.89	.87	.85	.89	.28	.24	.22	**1.00**	.87	1.00	.97	.96	.94	.89
.63	.74	.48	.43	.51	.45	.43	.42	.62	.83	.81	.83	.81	.79	.77	.79	.29	.29	.27	.87	**1.00**	.87	.90	.88	.86	.79
.75	.88	.50	.52	.53	.46	.43	.42	.65	.96	.88	.96	.89	.87	.85	.89	.28	.24	.22	1.00	.87	**1.00**	.97	.96	.94	.89
.76	.87	.46	.51	.49	.43	.39	.39	.63	.93	.90	.93	.91	.90	.88	.89	.27	.24	.22	.97	.90	.97	**1.00**	.99	.98	.89
.76	.88	.44	.50	.47	.41	.38	.37	.62	.91	.90	.91	.90	.90	.89	.89	.26	.22	.20	.96	.88	.96	.99	**1.00**	1.00	.90
.76	.87	.42	.49	.45	.39	.36	.35	.61	.90	.89	.90	.89	.90	.89	.89	.26	.22	.19	.94	.86	.94	.98	1.00	**1.00**	.89
.67	.95	.54	.35	.56	.50	.48	.47	.78	.85	.82	.85	.82	.82	.80	1.00	.24	.19	.17	.89	.79	.89	.89	.90	.89	**1.00**

Table C.2 Spearman rank correlation coefficients between 51 EH measures at 222 km × 222 km grain. Diagonal is marked in bold. Abbreviated measure names consist of three letters for each variable and two letters for calculation methods, e.g. ELE.sd, standard deviation of elevation. Variables: ELE, elevation; GLC, land cover classes; NPP, annual net primary production; PET, mean annual potential evapotranspiration; PLA, vascular plant species richness; PRE, annual precipitation; SOI, major soil groups; TEM, annual mean temperature; VEG, canopy height. Calculation methods: co, count; cv, coefficient of variation; ma, maximum; me, mean; ra, range; sd, standard deviation; sh, Shannon entropy; si, Simpson index; tr, terrain ruggedness index.

	GLC.co	GLC.sh	GLC.si	NPP.co	NPP.cv	NPP.ra	NPP.sd	NPP.sh	NPP.si	NPP.tr	PLA.co	VEG.co	VEG.cv	VEG.ma	VEG.me	VEG.ra	VEG.sd	VEG.sh	VEG.si	VEG.tr	PET.co	PET.cv	PET.ra	PET.sd	PET.sh
GLC.co	**1.00**	.66	.56	.42	-.20	.41	.46	.47	.46	.11	.22	.45	-.19	.46	.56	.46	.55	.56	.56	.49	.01	.39	.01	.03	.02
GLC.sh	.66	**1.00**	.98	.44	-.10	.43	.55	.60	.59	.25	.21	.41	-.05	.40	.44	.40	.60	.52	.50	.62	.15	.42	.15	.17	.17
GLC.si	.56	.98	**1.00**	.41	-.09	.40	.52	.56	.56	.25	.21	.38	.00	.36	.38	.36	.57	.49	.46	.59	.16	.38	.16	.18	.18
NPP.co	.42	.44	.41	**1.00**	-.38	.99	.90	.86	.82	.02	.76	.83	-.30	.83	.73	.83	.77	.75	.70	.72	.24	.18	.24	.20	.19
NPP.cv	-.20	-.10	-.09	-.38	**1.00**	-.39	-.16	-.19	-.19	.56	-.35	-.35	.41	-.37	-.52	-.37	-.29	-.45	-.47	-.31	.33	.29	.33	.35	.34
NPP.ra	.41	.43	.40	.99	-.39	**1.00**	.89	.85	.82	.01	.75	.82	-.30	.82	.73	.82	.76	.74	.69	.71	.24	.18	.24	.20	.19
NPP.sd	.46	.55	.52	.90	-.16	.89	**1.00**	.94	.91	.25	.65	.77	-.24	.75	.67	.75	.80	.74	.68	.74	.27	.30	.27	.26	.25
NPP.sh	.47	.60	.56	.86	-.19	.85	.94	**1.00**	.99	.18	.59	.71	-.21	.69	.62	.69	.76	.70	.65	.76	.29	.33	.29	.28	.27
NPP.si	.46	.59	.56	.82	-.19	.82	.91	.99	**1.00**	.17	.56	.68	-.20	.66	.61	.66	.74	.68	.64	.75	.28	.32	.27	.26	.26
NPP.tr	.11	.25	.25	.02	.56	.01	.25	.18	.17	**1.00**	.05	.05	.38	.03	-.11	.03	.13	-.04	-.06	.13	.34	.38	.34	.34	.33
PLA.co	.22	.21	.21	.76	-.35	.75	.65	.59	.56	.05	**1.00**	.75	-.14	.73	.55	.73	.60	.55	.49	.56	.28	.06	.28	.22	.21
VEG.co	.45	.41	.38	.83	-.35	.82	.77	.71	.68	.05	.75	**1.00**	-.28	.98	.77	.98	.82	.79	.71	.70	.30	.26	.30	.24	.23
VEG.cv	-.19	-.05	.00	-.30	.41	-.30	-.24	-.21	-.20	.38	-.14	-.28	**1.00**	-.32	-.60	-.32	-.26	-.53	-.57	-.20	.26	.13	.26	.26	.26
VEG.ma	.46	.40	.36	.83	-.37	.82	.75	.69	.66	.03	.73	.98	-.32	**1.00**	.81	1.00	.82	.79	.72	.69	.26	.26	.26	.20	.19
VEG.me	.56	.44	.38	.73	-.52	.73	.67	.62	.61	-.11	.55	.77	-.60	.81	**1.00**	.81	.79	.94	.93	.67	-.03	.14	-.03	-.06	-.07
VEG.ra	.46	.40	.36	.83	-.37	.82	.75	.69	.66	.03	.73	.98	-.32	1.00	.81	**1.00**	.82	.79	.72	.69	.26	.26	.26	.20	.19
VEG.sd	.55	.60	.57	.77	-.29	.76	.80	.76	.74	.13	.60	.82	-.26	.82	.79	.82	**1.00**	.84	.76	.89	.24	.36	.23	.21	.21
VEG.sh	.56	.52	.49	.75	-.45	.74	.74	.70	.68	-.04	.55	.79	-.53	.79	.94	.79	.84	**1.00**	.98	.76	.04	.18	.04	.02	.01
VEG.si	.56	.50	.46	.70	-.47	.69	.68	.65	.64	-.06	.49	.71	-.57	.72	.93	.72	.76	.98	**1.00**	.70	-.03	.14	-.03	-.05	-.05
VEG.tr	.49	.62	.59	.72	-.31	.71	.74	.76	.75	.13	.56	.70	-.20	.69	.67	.69	.89	.76	.70	**1.00**	.23	.33	.23	.22	.22
PET.co	.01	.15	.16	.24	.33	.24	.27	.29	.28	.34	.28	.30	.26	.26	-.03	.26	.24	.04	-.03	.23	**1.00**	.70	1.00	.93	.92
PET.cv	.39	.42	.38	.18	.29	.18	.30	.33	.32	.38	.06	.26	.13	.26	.14	.26	.36	.18	.14	.33	.70	**1.00**	.70	.79	.78
PET.ra	.01	.15	.16	.24	.33	.24	.27	.29	.27	.34	.28	.30	.26	.26	-.03	.26	.23	.04	-.03	.23	1.00	.70	**1.00**	.93	.92
PET.sd	.03	.17	.18	.20	.35	.20	.26	.28	.26	.34	.22	.24	.26	.20	-.06	.20	.21	.02	-.05	.22	.93	.79	.93	**1.00**	.99
PET.sh	.02	.17	.18	.19	.34	.19	.25	.27	.26	.33	.21	.23	.26	.19	-.07	.19	.21	.01	-.05	.22	.92	.78	.92	.99	**1.00**
PET.si	.03	.16	.18	.17	.33	.17	.23	.25	.24	.32	.18	.20	.25	.16	-.07	.16	.19	.01	-.05	.21	.87	.77	.87	.97	.99
PET.tr	.12	.21	.20	.36	.14	.35	.34	.35	.33	.22	.38	.46	.05	.45	.22	.45	.41	.24	.17	.38	.80	.58	.80	.70	.70
PRE.co	.25	.34	.33	.72	-.19	.71	.69	.67	.65	.18	.71	.72	-.10	.69	.53	.69	.64	.55	.49	.58	.47	.22	.47	.38	.37
PRE.cv	-.23	-.14	-.13	-.25	.57	-.26	-.20	-.18	-.19	.24	-.19	-.20	.34	-.24	-.47	-.24	-.23	-.40	-.45	-.27	.52	.29	.52	.48	.47
PRE.ra	.23	.31	.31	.70	-.16	.69	.67	.64	.62	.20	.70	.70	-.07	.67	.50	.67	.62	.52	.45	.55	.50	.23	.50	.41	.40
PRE.sd	.21	.30	.31	.68	-.16	.67	.65	.63	.61	.20	.67	.67	-.07	.64	.49	.64	.60	.51	.45	.54	.44	.19	.44	.36	.35
PRE.sh	.24	.33	.34	.70	-.21	.69	.68	.66	.64	.17	.68	.68	-.11	.65	.53	.65	.63	.55	.49	.58	.39	.17	.39	.32	.31
PRE.si	.23	.33	.33	.69	-.22	.68	.67	.65	.64	.17	.68	.67	-.11	.64	.53	.64	.62	.54	.49	.57	.38	.16	.38	.31	.30
PRE.tr	.36	.42	.40	.71	-.18	.71	.69	.68	.66	.18	.63	.74	-.16	.74	.61	.74	.71	.61	.54	.65	.56	.44	.56	.47	.47
TEM.co	.24	.29	.26	.24	.31	.23	.29	.31	.30	.36	.19	.34	.19	.32	.09	.32	.32	.13	.07	.27	.87	.80	.87	.79	.77
TEM.cv	.29	.34	.31	.19	.32	.19	.28	.31	.30	.37	.11	.27	.18	.26	.08	.26	.31	.13	.07	.28	.78	.87	.78	.79	.77
TEM.ra	.24	.29	.26	.24	.31	.23	.29	.31	.30	.36	.19	.34	.19	.32	.09	.32	.32	.13	.07	.27	.87	.80	.87	.79	.77
TEM.sd	.27	.32	.30	.20	.32	.19	.28	.31	.30	.36	.12	.27	.18	.26	.07	.26	.30	.12	.06	.28	.80	.86	.80	.80	.79
TEM.sh	.27	.33	.31	.18	.32	.18	.26	.30	.29	.36	.10	.25	.18	.24	.07	.24	.29	.12	.06	.28	.77	.86	.77	.79	.79
TEM.si	.27	.33	.31	.16	.31	.16	.25	.28	.28	.35	.07	.23	.17	.21	.07	.21	.28	.11	.06	.27	.72	.85	.72	.76	.77
TEM.tr	.27	.31	.28	.38	.11	.37	.37	.38	.36	.22	.34	.49	-.02	.50	.32	.50	.48	.32	.25	.42	.72	.66	.72	.64	.64
SOI.co	.23	.35	.33	.14	.11	.13	.17	.22	.23	.19	.04	.16	.13	.15	.11	.15	.24	.16	.13	.22	.33	.40	.33	.29	.28
SOI.sh	.27	.35	.34	.14	.11	.13	.18	.23	.23	.17	.03	.13	.09	.12	.10	.12	.21	.15	.14	.17	.27	.34	.27	.26	.25
SOI.si	.25	.32	.31	.12	.11	.11	.16	.20	.21	.14	.01	.10	.07	.09	.08	.09	.17	.13	.12	.14	.24	.30	.24	.24	.23
ELE.co	.17	.23	.22	.25	.29	.24	.27	.29	.28	.31	.23	.34	.19	.32	.08	.32	.30	.12	.05	.25	.86	.69	.86	.74	.72
ELE.cv	.26	.32	.29	.27	.20	.26	.31	.33	.31	.22	.19	.32	.09	.32	.16	.32	.35	.19	.13	.28	.69	.60	.69	.62	.59
ELE.ra	.17	.23	.22	.25	.29	.24	.27	.29	.28	.31	.23	.34	.19	.32	.08	.32	.30	.12	.05	.25	.86	.69	.86	.74	.72
ELE.sd	.16	.25	.23	.22	.29	.22	.26	.28	.26	.29	.20	.30	.18	.29	.06	.29	.29	.11	.04	.25	.83	.71	.83	.75	.73
ELE.sh	.15	.24	.23	.20	.28	.20	.23	.26	.25	.28	.17	.28	.18	.26	.06	.26	.28	.10	.04	.25	.80	.71	.80	.74	.73
ELE.si	.14	.23	.22	.18	.28	.18	.21	.25	.23	.26	.15	.25	.17	.24	.05	.24	.26	.09	.03	.25	.77	.70	.77	.72	.72
ELE.tr	.29	.33	.29	.40	.09	.39	.39	.40	.38	.21	.34	.51	-.04	.52	.35	.52	.50	.35	.28	.44	.71	.66	.71	.63	.63

PET.si	PET.tr	PRE.co	PRE.cv	PRE.ra	PRE.sd	PRE.sh	PRE.si	PRE.tr	TEM.co	TEM.cv	TEM.ra	TEM.sd	TEM.sh	TEM.si	TEM.tr	SOI.co	SOI.sh	SOI.si	ELE.co	ELE.cv	ELE.ra	ELE.sd	ELE.sh	ELE.si	ELE.tr
.03	.12	.25	-.23	.23	.21	.24	.23	.36	.24	.29	.24	.27	.27	.27	.27	.23	.27	.25	.17	.26	.17	.16	.15	.14	.29
.16	.21	.34	-.14	.31	.30	.33	.33	.42	.29	.34	.29	.32	.33	.33	.31	.35	.35	.32	.23	.32	.23	.25	.24	.23	.33
.18	.20	.33	-.13	.31	.31	.34	.33	.40	.26	.31	.26	.30	.31	.31	.28	.33	.34	.31	.22	.29	.22	.23	.23	.22	.29
.17	.36	.72	-.25	.70	.68	.70	.69	.71	.24	.19	.24	.20	.18	.16	.38	.14	.14	.12	.25	.27	.25	.22	.20	.18	.40
.33	.14	-.19	.57	-.16	-.16	-.21	-.22	-.18	.31	.32	.31	.32	.32	.31	.11	.11	.11	.11	.29	.20	.29	.29	.28	.28	.09
.17	.35	.71	-.26	.69	.67	.69	.68	.71	.23	.19	.23	.19	.18	.16	.37	.13	.13	.11	.24	.26	.24	.22	.20	.18	.39
.23	.34	.69	-.20	.67	.65	.68	.67	.69	.29	.28	.29	.28	.26	.25	.37	.17	.18	.16	.27	.31	.27	.26	.23	.21	.39
.25	.35	.67	-.18	.64	.63	.66	.65	.68	.31	.31	.31	.31	.30	.28	.38	.22	.23	.20	.29	.33	.29	.28	.26	.25	.40
.24	.33	.65	-.19	.62	.61	.64	.64	.66	.30	.30	.30	.30	.29	.28	.36	.23	.23	.21	.28	.31	.28	.26	.25	.23	.38
.32	.22	.18	.24	.20	.20	.17	.17	.18	.36	.37	.36	.36	.36	.35	.22	.19	.17	.14	.31	.22	.31	.29	.28	.26	.21
.18	.38	.71	-.19	.70	.67	.68	.68	.63	.19	.11	.19	.12	.10	.07	.34	.04	.03	.01	.23	.19	.23	.20	.17	.15	.34
.20	.46	.72	-.20	.70	.67	.68	.67	.74	.34	.27	.34	.27	.25	.23	.49	.16	.13	.10	.34	.32	.34	.30	.28	.25	.51
.25	.05	-.10	.34	-.07	-.07	-.11	-.11	-.16	.19	.18	.19	.18	.18	.17	-.02	.13	.09	.07	.19	.09	.19	.18	.18	.17	-.04
.16	.45	.69	-.24	.67	.64	.65	.64	.74	.32	.26	.32	.26	.24	.21	.50	.15	.12	.09	.32	.32	.32	.29	.26	.24	.52
-.07	.22	.53	-.47	.50	.49	.53	.53	.61	.09	.08	.09	.07	.07	.07	.32	.11	.10	.08	.08	.16	.08	.06	.06	.05	.35
.16	.45	.69	-.24	.67	.64	.65	.64	.74	.32	.26	.32	.26	.24	.21	.50	.15	.12	.09	.32	.32	.32	.29	.26	.24	.52
.19	.41	.64	-.23	.62	.60	.63	.62	.71	.32	.31	.32	.30	.29	.28	.48	.24	.21	.17	.30	.35	.30	.29	.28	.26	.50
.01	.24	.55	-.40	.52	.51	.55	.54	.61	.13	.13	.13	.12	.12	.11	.32	.16	.15	.13	.12	.19	.12	.11	.10	.09	.35
-.05	.17	.49	-.45	.45	.45	.49	.49	.54	.07	.07	.07	.06	.06	.06	.25	.13	.14	.12	.05	.13	.05	.04	.04	.03	.28
.21	.38	.58	-.27	.55	.54	.58	.57	.65	.27	.28	.27	.28	.28	.27	.42	.22	.17	.14	.25	.28	.25	.25	.25	.25	.44
.87	.80	.47	.52	.50	.44	.39	.38	.56	.87	.78	.87	.80	.77	.72	.72	.33	.27	.24	.86	.69	.86	.83	.80	.77	.71
.77	.58	.22	.29	.23	.19	.17	.16	.44	.80	.87	.80	.86	.86	.85	.66	.40	.34	.30	.69	.60	.69	.71	.71	.70	.66
.87	.80	.47	.52	.50	.44	.39	.38	.56	.87	.78	.87	.80	.77	.72	.72	.33	.27	.24	.86	.69	.86	.83	.80	.77	.71
.97	.70	.38	.48	.41	.36	.32	.31	.47	.79	.79	.79	.80	.79	.76	.64	.29	.26	.24	.74	.62	.74	.75	.74	.72	.63
.99	.70	.37	.47	.40	.35	.31	.30	.47	.77	.77	.77	.79	.79	.77	.64	.28	.25	.23	.72	.59	.72	.73	.73	.72	.63
1.00	.66	.33	.44	.36	.31	.28	.27	.44	.72	.74	.73	.76	.77	.76	.60	.26	.23	.21	.67	.54	.66	.68	.70	.69	.59
.66	**1.00**	.55	.38	.58	.51	.48	.46	.77	.79	.72	.79	.73	.73	.69	.96	.28	.20	.17	.85	.71	.85	.86	.87	.86	.95
.33	.55	**1.00**	.16	.99	.97	.97	.96	.85	.40	.29	.41	.31	.28	.24	.51	.18	.16	.14	.45	.42	.45	.40	.37	.34	.50
.44	.38	.16	**1.00**	.21	.23	.15	.15	.07	.45	.39	.45	.40	.38	.35	.30	.15	.13	.11	.50	.39	.50	.49	.48	.46	.28
.36	.58	.99	.21	**1.00**	.97	.96	.95	.85	.43	.31	.43	.33	.30	.26	.53	.19	.16	.14	.48	.44	.48	.43	.40	.37	.52
.31	.51	.97	.23	.97	**1.00**	.99	.99	.79	.35	.25	.35	.27	.24	.20	.45	.16	.15	.13	.40	.38	.40	.36	.33	.30	.45
.28	.48	.97	.15	.96	.99	**1.00**	1.00	.79	.32	.23	.32	.24	.21	.18	.43	.15	.15	.13	.37	.35	.37	.32	.29	.27	.43
.27	.46	.96	.15	.95	.99	1.00	**1.00**	.78	.31	.21	.31	.23	.20	.17	.42	.15	.15	.13	.35	.34	.35	.31	.28	.26	.42
.44	.77	.85	.07	.85	.79	.79	.78	**1.00**	.58	.51	.58	.52	.50	.47	.78	.26	.21	.18	.62	.57	.62	.60	.59	.57	.78
.72	.79	.40	.45	.43	.35	.32	.31	.58	**1.00**	.93	1.00	.94	.91	.87	.81	.40	.33	.29	.94	.80	.94	.90	.88	.84	.80
.74	.72	.29	.39	.31	.25	.23	.21	.51	.93	**1.00**	.93	1.00	.99	.97	.76	.38	.33	.29	.82	.75	.82	.86	.85	.83	.76
.73	.79	.41	.45	.43	.35	.32	.31	.58	1.00	.93	**1.00**	.94	.91	.87	.81	.40	.33	.29	.94	.80	.94	.90	.88	.84	.80
.76	.73	.31	.40	.33	.27	.24	.23	.52	.94	1.00	.94	**1.00**	.99	.96	.76	.37	.33	.29	.83	.76	.83	.86	.85	.83	.76
.77	.73	.28	.38	.30	.24	.21	.20	.50	.91	.99	.91	.99	**1.00**	.99	.76	.37	.31	.28	.80	.71	.80	.84	.85	.84	.76
.76	.69	.24	.35	.26	.20	.18	.17	.47	.87	.97	.87	.96	.99	**1.00**	.73	.35	.29	.26	.75	.66	.75	.79	.82	.82	.72
.60	.96	.51	.30	.53	.45	.43	.42	.78	.81	.76	.81	.76	.76	.73	**1.00**	.32	.24	.20	.85	.75	.85	.86	.87	.86	1.00
.26	.28	.18	.15	.19	.16	.15	.15	.26	.40	.38	.40	.37	.37	.35	.32	**1.00**	.75	.63	.37	.33	.37	.34	.33	.31	.31
.23	.20	.16	.13	.16	.15	.15	.15	.21	.33	.33	.33	.33	.31	.29	.24	.75	**1.00**	.97	.29	.34	.29	.28	.25	.23	.23
.21	.17	.14	.11	.14	.13	.13	.13	.18	.29	.29	.29	.29	.28	.26	.20	.63	.97	**1.00**	.25	.31	.25	.24	.22	.20	.19
.67	.85	.45	.50	.48	.40	.37	.35	.62	.94	.82	.94	.83	.80	.75	.85	.37	.29	.25	**1.00**	.84	1.00	.96	.93	.90	.85
.54	.71	.42	.39	.44	.38	.35	.34	.57	.80	.75	.80	.76	.71	.66	.75	.33	.34	.31	.84	**1.00**	.84	.88	.84	.81	.74
.66	.85	.45	.50	.48	.40	.37	.35	.62	.94	.82	.94	.83	.80	.75	.85	.37	.29	.25	1.00	.84	**1.00**	.96	.93	.90	.85
.68	.86	.40	.49	.43	.36	.32	.31	.60	.90	.86	.90	.86	.84	.79	.86	.34	.28	.24	.96	.88	.96	**1.00**	.98	.96	.86
.70	.87	.37	.48	.40	.33	.29	.28	.59	.88	.85	.88	.85	.85	.82	.87	.33	.25	.22	.93	.84	.93	.98	**1.00**	.99	.87
.69	.86	.34	.46	.37	.30	.27	.26	.57	.84	.83	.84	.83	.84	.82	.86	.31	.23	.20	.90	.81	.90	.96	.99	**1.00**	.86
.59	.95	.50	.28	.52	.45	.43	.42	.78	.80	.76	.80	.76	.76	.72	1.00	.31	.23	.19	.85	.74	.85	.86	.87	.86	**1.00**

Table C.3 Spearman rank correlation coefficients between 51 EH measures at 444 km × 444 km grain. Diagonal is marked in bold. Abbreviated measure names consist of three letters for each variable and two letters for calculation methods, e.g. ELE.sd, standard deviation of elevation. Variables: ELE, elevation; GLC, land cover classes; NPP, annual net primary production; PET, mean annual potential evapotranspiration; PLA, vascular plant species richness; PRE, annual precipitation; SOI, major soil groups; TEM, annual mean temperature; VEG, canopy height. Calculation methods: co, count; cv, coefficient of variation; ma, maximum; me, mean; ra, range; sd, standard deviation; sh, Shannon entropy; si, Simpson index; tr, terrain ruggedness index.

	GLC.co	GLC.sh	GLC.si	NPP.co	NPP.cv	NPP.ra	NPP.sd	NPP.sh	NPP.si	NPP.tr	PLA.co	VEG.co	VEG.cv	VEG.ma	VEG.me	VEG.ra	VEG.sd	VEG.sh	VEG.si	VEG.tr	PET.co	PET.cv	PET.ra	PET.sd	PET.sh
GLC.co	**1.00**	.67	.56	.37	-.31	.37	.44	.45	.46	.04	.24	.41	-.36	.44	.55	.44	.55	.56	.55	.47	.01	.50	.01	.10	.09
GLC.sh	.67	**1.00**	.97	.41	-.23	.41	.53	.59	.60	.20	.23	.36	-.25	.36	.44	.36	.57	.51	.50	.61	.15	.43	.15	.19	.19
GLC.si	.56	.97	**1.00**	.38	-.20	.38	.51	.56	.57	.23	.24	.32	-.18	.31	.37	.31	.52	.46	.44	.59	.17	.37	.17	.20	.20
NPP.co	.37	.41	.38	**1.00**	-.48	1.00	.91	.86	.82	-.04	.78	.81	-.46	.81	.71	.81	.77	.70	.65	.71	.26	.14	.25	.18	.18
NPP.cv	-.31	-.23	-.20	-.48	**1.00**	-.47	-.35	-.39	-.40	.50	-.49	-.47	.57	-.50	-.68	-.50	-.47	-.65	-.66	-.49	.34	.23	.35	.38	.37
NPP.ra	.37	.41	.38	1.00	-.47	**1.00**	.90	.85	.81	-.03	.78	.81	-.45	.80	.70	.80	.76	.69	.64	.70	.26	.14	.25	.18	.18
NPP.sd	.44	.53	.51	.91	-.35	.90	**1.00**	.94	.90	.11	.68	.75	-.46	.75	.70	.75	.80	.72	.68	.73	.27	.23	.27	.23	.23
NPP.sh	.45	.59	.56	.86	-.39	.85	.94	**1.00**	.99	.04	.62	.69	-.46	.69	.68	.69	.76	.71	.67	.75	.25	.23	.25	.21	.21
NPP.si	.46	.60	.57	.82	-.40	.81	.90	.99	**1.00**	.03	.58	.65	-.46	.65	.67	.65	.73	.70	.67	.74	.22	.23	.22	.20	.19
NPP.tr	.04	.20	.23	-.04	.50	-.03	.11	.04	.03	**1.00**	-.02	-.01	.41	-.04	-.22	-.04	.02	-.18	-.20	.05	.40	.38	.40	.40	.40
PLA.co	.24	.23	.24	.78	-.49	.78	.68	.62	.58	-.02	**1.00**	.75	-.35	.74	.60	.74	.66	.58	.51	.60	.24	.02	.24	.14	.15
VEG.co	.41	.36	.32	.81	-.47	.81	.75	.69	.65	-.01	.75	**1.00**	-.45	.98	.73	.98	.79	.72	.66	.63	.26	.20	.26	.16	.17
VEG.cv	-.36	-.25	-.18	-.46	.57	-.45	-.46	-.46	-.46	.41	-.35	-.45	**1.00**	-.49	-.79	-.49	-.49	-.76	-.79	-.41	.30	.09	.30	.31	.30
VEG.ma	.44	.36	.31	.81	-.50	.80	.75	.69	.65	-.04	.74	.98	-.49	**1.00**	.77	1.00	.80	.74	.68	.63	.21	.20	.21	.12	.12
VEG.me	.55	.44	.37	.71	-.68	.70	.70	.68	.67	-.22	.60	.73	-.79	.77	**1.00**	.77	.81	.96	.94	.66	-.12	.10	-.12	-.15	-.15
VEG.ra	.44	.36	.31	.81	-.50	.80	.75	.69	.65	-.04	.74	.98	-.49	1.00	.77	**1.00**	.80	.74	.68	.63	.21	.20	.21	.12	.12
VEG.sd	.55	.57	.52	.77	-.47	.76	.80	.76	.73	.02	.66	.79	-.49	.80	.81	.80	**1.00**	.84	.76	.85	.18	.29	.18	.13	.13
VEG.sh	.56	.51	.46	.70	-.65	.69	.72	.71	.70	-.18	.58	.72	-.76	.74	.96	.74	.84	**1.00**	.98	.72	-.09	.11	-.09	-.11	-.11
VEG.si	.55	.50	.44	.65	-.66	.64	.68	.67	.67	-.20	.51	.66	-.79	.68	.94	.68	.76	.98	**1.00**	.67	-.15	.07	-.15	-.17	-.17
VEG.tr	.47	.61	.59	.71	-.49	.70	.73	.75	.74	.05	.60	.63	-.41	.63	.66	.63	.85	.72	.67	**1.00**	.19	.28	.18	.16	.18
PET.co	.01	.15	.17	.26	.34	.26	.27	.25	.22	.40	.24	.26	.30	.21	-.12	.21	.18	-.09	-.15	.19	**1.00**	.62	1.00	.87	.86
PET.cv	.50	.43	.37	.14	.23	.14	.23	.23	.23	.38	.02	.20	.09	.20	.10	.20	.29	.11	.07	.28	.62	**1.00**	.62	.77	.76
PET.ra	.01	.15	.17	.25	.35	.25	.27	.25	.22	.40	.24	.26	.30	.21	-.12	.21	.18	-.09	-.15	.18	1.00	.62	**1.00**	.88	.86
PET.sd	.10	.19	.20	.18	.38	.18	.23	.21	.20	.40	.14	.16	.31	.12	-.15	.12	.13	-.11	-.17	.16	.87	.77	.88	**1.00**	.98
PET.sh	.09	.19	.20	.18	.37	.18	.23	.21	.19	.40	.15	.17	.30	.12	-.15	.12	.13	-.11	-.17	.18	.86	.76	.86	.98	**1.00**
PET.si	.11	.19	.21	.14	.35	.15	.20	.18	.17	.38	.11	.14	.29	.10	-.15	.10	.11	-.11	-.16	.17	.78	.75	.78	.94	.98
PET.tr	.13	.22	.20	.38	.08	.36	.36	.34	.30	.26	.39	.47	.01	.44	.20	.44	.42	.18	.10	.36	.76	.50	.76	.60	.61
PRE.co	.23	.32	.33	.75	-.31	.74	.72	.67	.63	.15	.73	.72	-.28	.69	.54	.69	.66	.52	.46	.56	.39	.08	.39	.23	.22
PRE.cv	-.28	-.18	-.16	-.31	.76	-.31	-.28	-.31	-.32	.37	-.31	-.30	.56	-.36	-.60	-.36	-.35	-.58	-.62	-.40	.47	.19	.47	.41	.39
PRE.ra	.20	.30	.31	.73	-.27	.72	.70	.65	.61	.17	.72	.71	-.25	.67	.51	.67	.64	.49	.43	.54	.42	.08	.41	.25	.24
PRE.sd	.17	.30	.32	.70	-.24	.69	.69	.65	.61	.20	.68	.65	-.23	.61	.47	.61	.60	.46	.41	.51	.35	.02	.35	.20	.19
PRE.sh	.20	.33	.35	.72	-.31	.71	.72	.69	.65	.16	.70	.66	-.29	.63	.52	.63	.63	.51	.47	.55	.30	-.01	.30	.16	.15
PRE.si	.19	.32	.35	.70	-.32	.69	.71	.68	.65	.16	.69	.64	-.29	.61	.51	.61	.62	.51	.46	.55	.28	-.02	.28	.14	.14
PRE.tr	.38	.43	.39	.72	-.33	.71	.70	.67	.63	.12	.66	.75	-.34	.73	.62	.73	.73	.59	.53	.64	.51	.37	.51	.38	.38
TEM.co	.28	.27	.23	.19	.31	.19	.23	.22	.20	.42	.11	.26	.21	.23	.00	.23	.24	.00	-.06	.18	.85	.78	.85	.75	.73
TEM.cv	.38	.33	.28	.12	.30	.12	.19	.19	.19	.41	.02	.18	.19	.16	.00	.16	.21	.00	-.05	.18	.71	.88	.71	.76	.74
TEM.ra	.28	.27	.23	.19	.31	.19	.23	.22	.20	.42	.11	.26	.21	.23	.00	.23	.24	.00	-.06	.18	.85	.78	.85	.75	.73
TEM.sd	.36	.32	.27	.13	.30	.13	.20	.20	.19	.42	.03	.18	.20	.16	-.01	.16	.21	-.01	-.06	.18	.73	.87	.73	.77	.75
TEM.sh	.36	.33	.27	.10	.29	.10	.17	.17	.17	.40	.01	.16	.20	.15	-.01	.15	.20	-.02	-.06	.19	.69	.87	.69	.74	.76
TEM.si	.37	.32	.27	.07	.27	.07	.14	.15	.14	.38	-.02	.12	.20	.11	-.02	.11	.17	-.02	-.07	.19	.61	.85	.61	.70	.72
TEM.tr	.28	.30	.25	.38	.03	.37	.37	.35	.31	.23	.37	.49	-.08	.48	.30	.48	.48	.26	.19	.38	.69	.58	.69	.56	.57
SOI.co	.37	.48	.46	.22	.07	.22	.27	.30	.31	.27	.10	.23	.01	.22	.15	.22	.30	.20	.17	.29	.41	.52	.40	.40	.39
SOI.sh	.42	.49	.46	.18	.07	.18	.28	.30	.31	.22	.07	.19	-.03	.17	.16	.17	.24	.21	.20	.20	.31	.43	.31	.34	.31
SOI.si	.38	.43	.40	.15	.05	.14	.24	.26	.27	.16	.04	.16	-.04	.15	.15	.15	.21	.20	.20	.16	.26	.38	.26	.29	.26
ELE.co	.16	.20	.18	.23	.28	.23	.24	.22	.20	.37	.20	.30	.21	.26	.00	.26	.24	.00	-.07	.16	.86	.61	.86	.68	.66
ELE.cv	.25	.28	.23	.24	.19	.23	.28	.27	.25	.29	.17	.26	.10	.25	.09	.25	.29	.08	.02	.19	.68	.54	.68	.57	.53
ELE.ra	.16	.20	.18	.23	.28	.23	.24	.22	.20	.37	.20	.30	.21	.26	.00	.26	.24	.00	-.07	.16	.86	.61	.86	.68	.66
ELE.sd	.16	.23	.20	.22	.26	.22	.24	.23	.21	.36	.19	.28	.19	.24	.00	.24	.25	.00	-.06	.19	.83	.63	.83	.69	.67
ELE.sh	.13	.21	.19	.18	.26	.18	.20	.19	.16	.34	.16	.24	.21	.21	-.03	.21	.21	-.03	-.09	.18	.80	.62	.80	.67	.69
ELE.si	.12	.20	.18	.16	.25	.15	.17	.16	.14	.32	.15	.21	.20	.18	-.04	.18	.19	-.04	-.10	.18	.75	.60	.75	.64	.66
ELE.tr	.31	.31	.26	.40	.01	.39	.39	.37	.34	.22	.38	.51	-.10	.50	.33	.50	.50	.29	.22	.40	.67	.59	.67	.55	.56

PET.si	PET.tr	PRE.co	PRE.cv	PRE.ra	PRE.sd	PRE.sh	PRE.si	PRE.tr	TEM.co	TEM.cv	TEM.ra	TEM.sd	TEM.sh	TEM.si	TEM.tr	SOI.co	SOI.sh	SOI.si	ELE.co	ELE.cv	ELE.ra	ELE.sd	ELE.sh	ELE.si	ELE.tr
.11	.13	.23	-.28	.20	.17	.20	.19	.38	.28	.38	.28	.36	.36	.37	.28	.37	.42	.38	.16	.25	.16	.16	.13	.12	.31
.19	.22	.32	-.18	.30	.30	.33	.32	.43	.27	.33	.27	.32	.33	.32	.30	.48	.49	.43	.20	.28	.20	.23	.21	.20	.31
.21	.20	.33	-.16	.31	.32	.35	.35	.39	.23	.28	.23	.27	.27	.27	.25	.46	.46	.40	.18	.23	.18	.20	.19	.18	.26
.14	.38	.75	-.31	.73	.70	.72	.70	.72	.19	.12	.19	.13	.10	.07	.38	.22	.18	.15	.23	.24	.23	.22	.18	.16	.40
.35	.08	-.31	.76	-.27	-.24	-.31	-.32	-.33	.31	.30	.31	.30	.29	.27	.03	.07	.07	.05	.28	.19	.28	.26	.26	.25	.01
.15	.36	.74	-.31	.72	.69	.71	.69	.71	.19	.12	.19	.13	.10	.07	.37	.22	.18	.14	.23	.23	.23	.22	.18	.15	.39
.20	.36	.72	-.28	.70	.69	.72	.71	.70	.23	.19	.23	.20	.17	.14	.37	.27	.28	.24	.24	.28	.24	.24	.20	.17	.39
.18	.34	.67	-.31	.65	.65	.69	.68	.67	.22	.19	.22	.20	.17	.15	.35	.30	.30	.26	.22	.27	.22	.23	.19	.16	.37
.17	.30	.63	-.32	.61	.61	.65	.65	.63	.20	.19	.20	.19	.17	.14	.31	.31	.31	.27	.20	.25	.20	.21	.16	.14	.34
.38	.26	.15	.37	.17	.20	.16	.16	.12	.42	.41	.42	.42	.40	.38	.23	.27	.22	.16	.37	.29	.37	.36	.34	.32	.22
.11	.39	.73	-.31	.72	.68	.70	.69	.66	.11	.02	.11	.03	.01	-.02	.37	.10	.07	.04	.20	.17	.20	.19	.16	.15	.38
.14	.47	.72	-.30	.71	.65	.66	.64	.75	.26	.18	.26	.18	.16	.12	.49	.23	.19	.16	.30	.26	.30	.28	.24	.21	.51
.29	.01	-.28	.56	-.25	-.23	-.29	-.29	-.34	.21	.19	.21	.20	.20	.20	-.08	.01	-.03	-.04	.21	.10	.21	.19	.21	.20	-.10
.10	.44	.69	-.36	.67	.61	.63	.61	.73	.23	.16	.23	.16	.15	.11	.48	.22	.17	.15	.26	.25	.26	.24	.21	.18	.50
-.15	.20	.54	-.60	.51	.47	.52	.51	.62	.00	.00	.00	-.01	-.01	-.02	.30	.15	.16	.15	.00	.09	.00	.00	-.03	-.04	.33
.10	.44	.69	-.36	.67	.61	.63	.61	.73	.23	.16	.23	.16	.15	.11	.48	.22	.17	.15	.26	.25	.26	.24	.21	.18	.50
.11	.42	.66	-.35	.64	.60	.63	.62	.73	.24	.21	.24	.21	.20	.17	.48	.30	.24	.21	.24	.29	.24	.25	.21	.19	.50
-.11	.18	.52	-.58	.49	.46	.51	.51	.59	.00	.00	.00	-.01	-.02	-.02	.26	.20	.21	.20	.00	.08	.00	.00	-.03	-.04	.29
-.16	.10	.46	-.62	.43	.41	.47	.46	.53	-.06	-.05	-.06	-.06	-.06	-.07	.19	.17	.20	.20	-.07	.02	-.07	-.06	-.09	-.10	.22
.17	.36	.56	-.40	.54	.51	.55	.55	.64	.18	.18	.18	.18	.19	.19	.38	.29	.20	.16	.16	.19	.16	.19	.18	.18	.40
.78	.76	.39	.47	.42	.35	.30	.28	.51	.85	.71	.85	.73	.69	.61	.69	.41	.31	.26	.86	.68	.86	.83	.80	.75	.67
.75	.50	.08	.19	.08	.02	-.01	-.02	.37	.78	.88	.78	.87	.87	.85	.58	.52	.43	.38	.61	.54	.61	.63	.62	.60	.59
.78	.76	.39	.47	.41	.35	.30	.28	.51	.85	.71	.85	.73	.69	.61	.69	.40	.31	.26	.86	.68	.86	.83	.80	.75	.67
.94	.60	.23	.41	.25	.20	.16	.14	.38	.75	.76	.75	.77	.74	.70	.56	.40	.34	.29	.68	.57	.68	.69	.67	.64	.55
.98	.61	.22	.39	.24	.19	.15	.14	.38	.73	.74	.73	.75	.76	.72	.57	.39	.31	.26	.66	.53	.66	.67	.69	.66	.56
1.00	.54	.17	.35	.19	.15	.11	.10	.34	.67	.71	.67	.71	.74	.73	.51	.37	.29	.25	.59	.46	.59	.60	.63	.62	.50
.54	**1.00**	.53	.28	.55	.46	.43	.40	.79	.74	.63	.74	.64	.63	.57	.96	.41	.24	.18	.82	.69	.82	.86	.87	.84	.95
.17	.53	**1.00**	.01	1.00	.95	.94	.92	.81	.28	.13	.28	.14	.10	.04	.48	.25	.21	.17	.39	.34	.39	.34	.29	.26	.48
.35	.28	.01	**1.00**	.05	.10	.00	.00	-.09	.40	.31	.40	.32	.29	.24	.21	.15	.12	.10	.46	.35	.46	.44	.43	.41	.18
.19	.55	1.00	.05	**1.00**	.95	.94	.91	.81	.30	.14	.30	.15	.11	.05	.49	.25	.21	.17	.41	.36	.41	.37	.32	.28	.49
.15	.46	.95	.10	.95	**1.00**	.99	.98	.72	.22	.07	.22	.09	.05	-.01	.39	.23	.20	.16	.32	.28	.32	.29	.24	.21	.39
.11	.43	.94	.00	.94	.99	**1.00**	1.00	.72	.18	.04	.18	.06	.02	-.03	.37	.21	.19	.15	.28	.25	.28	.25	.20	.17	.37
.10	.40	.92	.00	.91	.98	1.00	**1.00**	.70	.15	.02	.15	.04	.00	-.05	.34	.21	.18	.15	.25	.23	.25	.23	.18	.15	.34
.34	.79	.81	-.09	.81	.72	.72	.70	**1.00**	.52	.43	.52	.44	.42	.36	.80	.38	.29	.24	.57	.53	.57	.60	.57	.55	.80
.67	.74	.28	.40	.30	.22	.18	.15	.52	**1.00**	.91	1.00	.91	.88	.81	.76	.51	.43	.37	.91	.77	.91	.88	.84	.79	.75
.71	.63	.13	.31	.14	.07	.04	.02	.43	.91	**1.00**	.91	1.00	.98	.94	.68	.49	.42	.37	.75	.70	.75	.79	.78	.74	.68
.67	.74	.28	.40	.30	.22	.18	.15	.52	1.00	.91	**1.00**	.91	.88	.81	.76	.51	.43	.37	.91	.77	.91	.88	.84	.79	.76
.71	.64	.14	.32	.15	.09	.06	.04	.44	.91	1.00	.91	**1.00**	.98	.94	.69	.48	.42	.36	.76	.71	.76	.80	.78	.75	.68
.74	.63	.10	.29	.11	.05	.02	.00	.42	.88	.98	.88	.98	**1.00**	.98	.68	.48	.40	.34	.72	.65	.72	.76	.78	.77	.68
.73	.57	.04	.24	.05	-.01	-.03	-.05	.36	.81	.94	.81	.94	.98	**1.00**	.62	.45	.37	.32	.64	.57	.64	.69	.73	.74	.62
.51	.96	.48	.21	.49	.39	.37	.34	.80	.76	.68	.76	.69	.68	.62	**1.00**	.45	.30	.24	.81	.71	.81	.85	.85	.83	.99
.37	.41	.25	.15	.25	.23	.21	.21	.38	.51	.49	.51	.48	.48	.45	.45	**1.00**	.74	.59	.48	.40	.48	.46	.44	.42	.45
.29	.24	.21	.12	.21	.20	.19	.18	.29	.43	.42	.43	.42	.40	.37	.30	.74	**1.00**	.96	.36	.42	.36	.34	.30	.27	.29
.25	.18	.17	.10	.17	.16	.15	.15	.24	.37	.37	.37	.36	.34	.32	.24	.59	.96	**1.00**	.28	.37	.28	.27	.23	.20	.22
.59	.82	.39	.46	.41	.32	.28	.25	.57	.91	.75	.91	.76	.72	.64	.81	.48	.36	.28	**1.00**	.82	1.00	.95	.90	.85	.80
.46	.69	.34	.35	.36	.28	.25	.23	.53	.77	.70	.77	.71	.65	.57	.71	.40	.42	.37	.82	**1.00**	.82	.88	.81	.76	.71
.59	.82	.39	.46	.41	.32	.28	.25	.57	.91	.75	.91	.76	.72	.64	.81	.48	.36	.28	1.00	.82	**1.00**	.95	.90	.85	.80
.60	.86	.34	.44	.37	.29	.25	.23	.60	.88	.79	.88	.80	.76	.69	.85	.46	.34	.27	.95	.88	.95	**1.00**	.98	.94	.85
.63	.87	.29	.43	.32	.24	.20	.18	.57	.84	.78	.84	.78	.78	.73	.85	.44	.30	.23	.90	.81	.90	.98	**1.00**	.99	.85
.62	.84	.26	.41	.28	.21	.17	.15	.55	.79	.74	.79	.75	.77	.74	.83	.42	.27	.20	.85	.76	.85	.94	.99	**1.00**	.83
.50	.95	.48	.18	.49	.39	.37	.34	.80	.75	.68	.76	.68	.68	.62	.99	.45	.29	.22	.80	.71	.80	.85	.85	.83	**1.00**

C.3 Global maps of EH measures

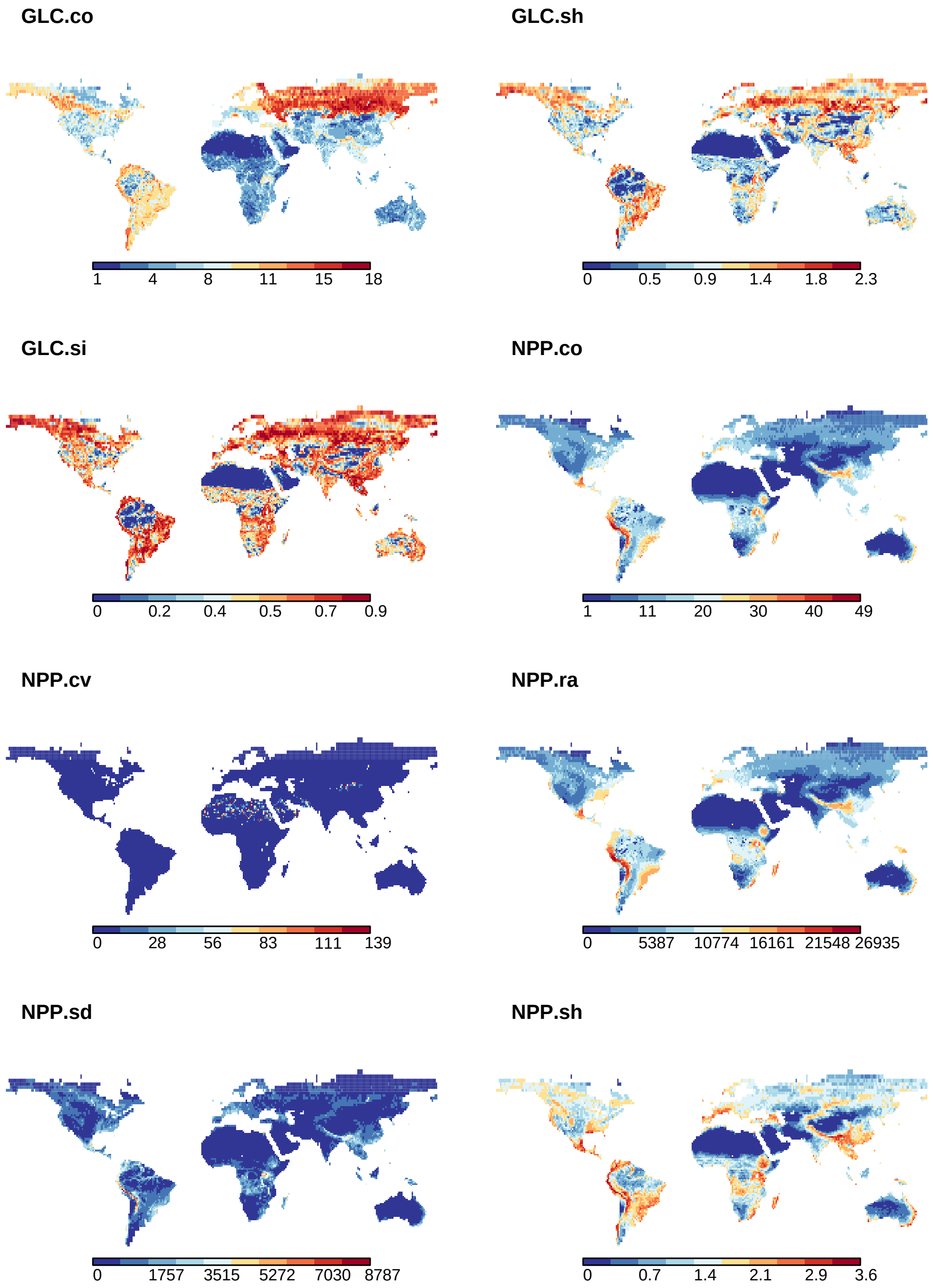
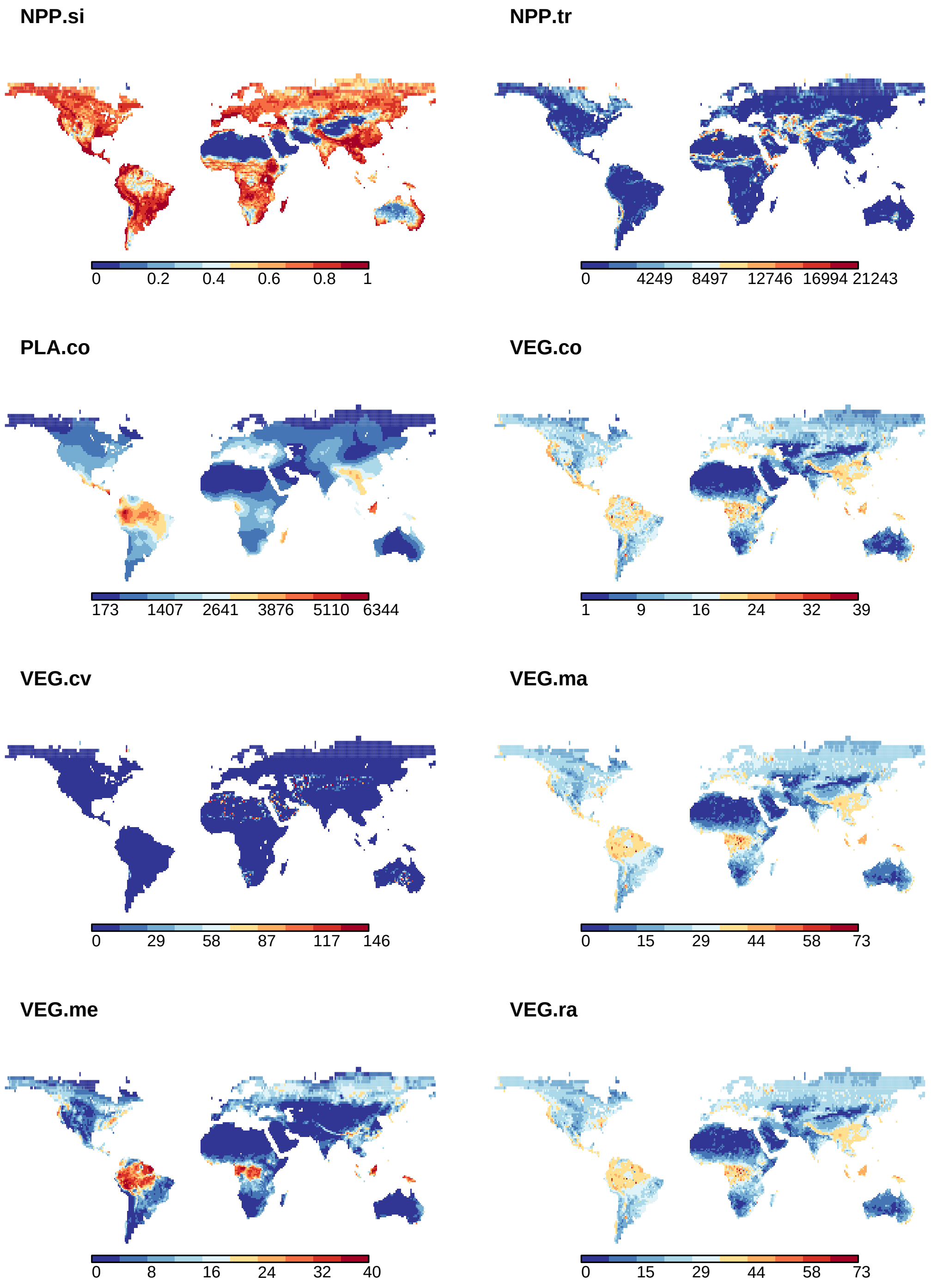
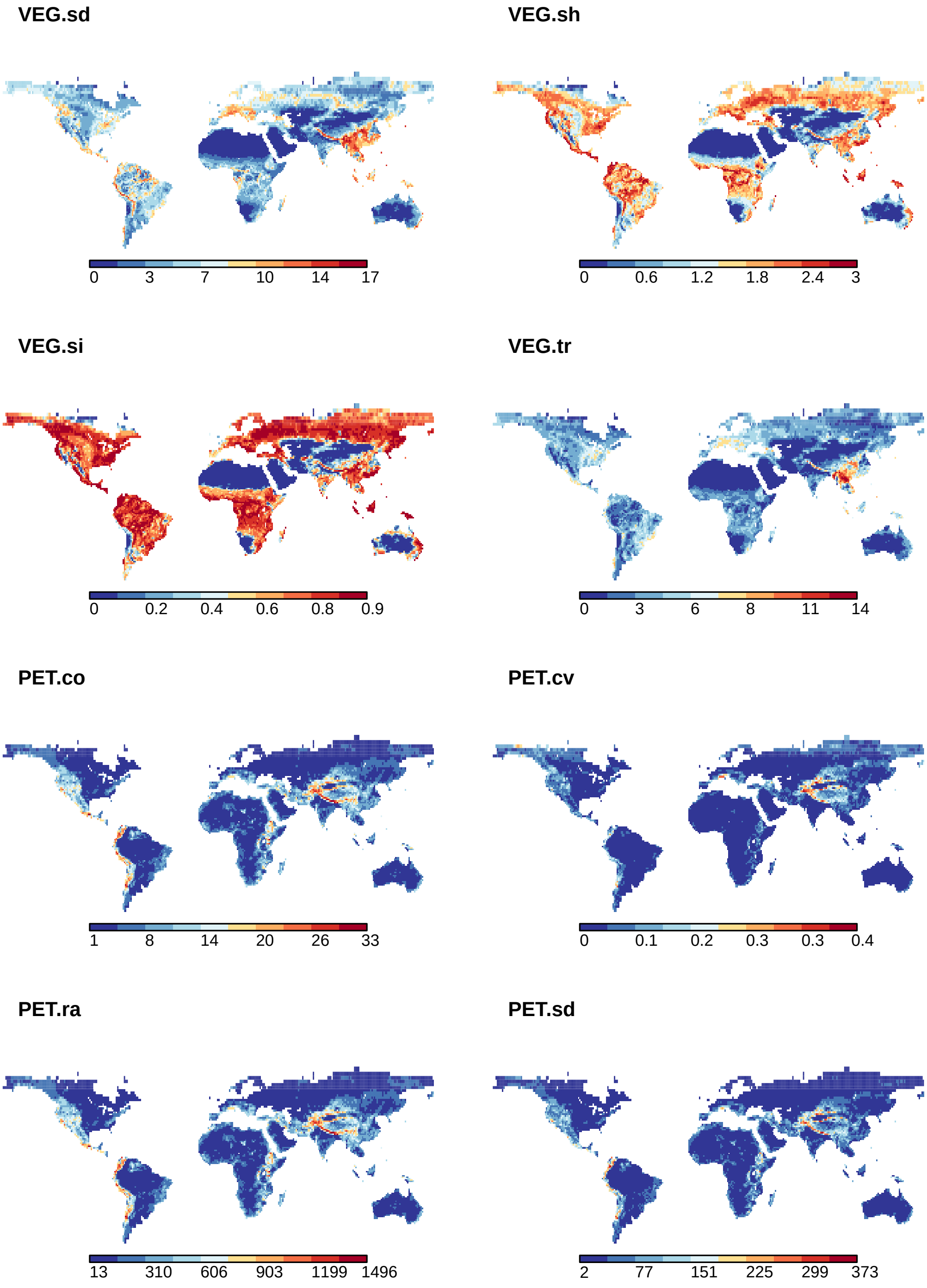


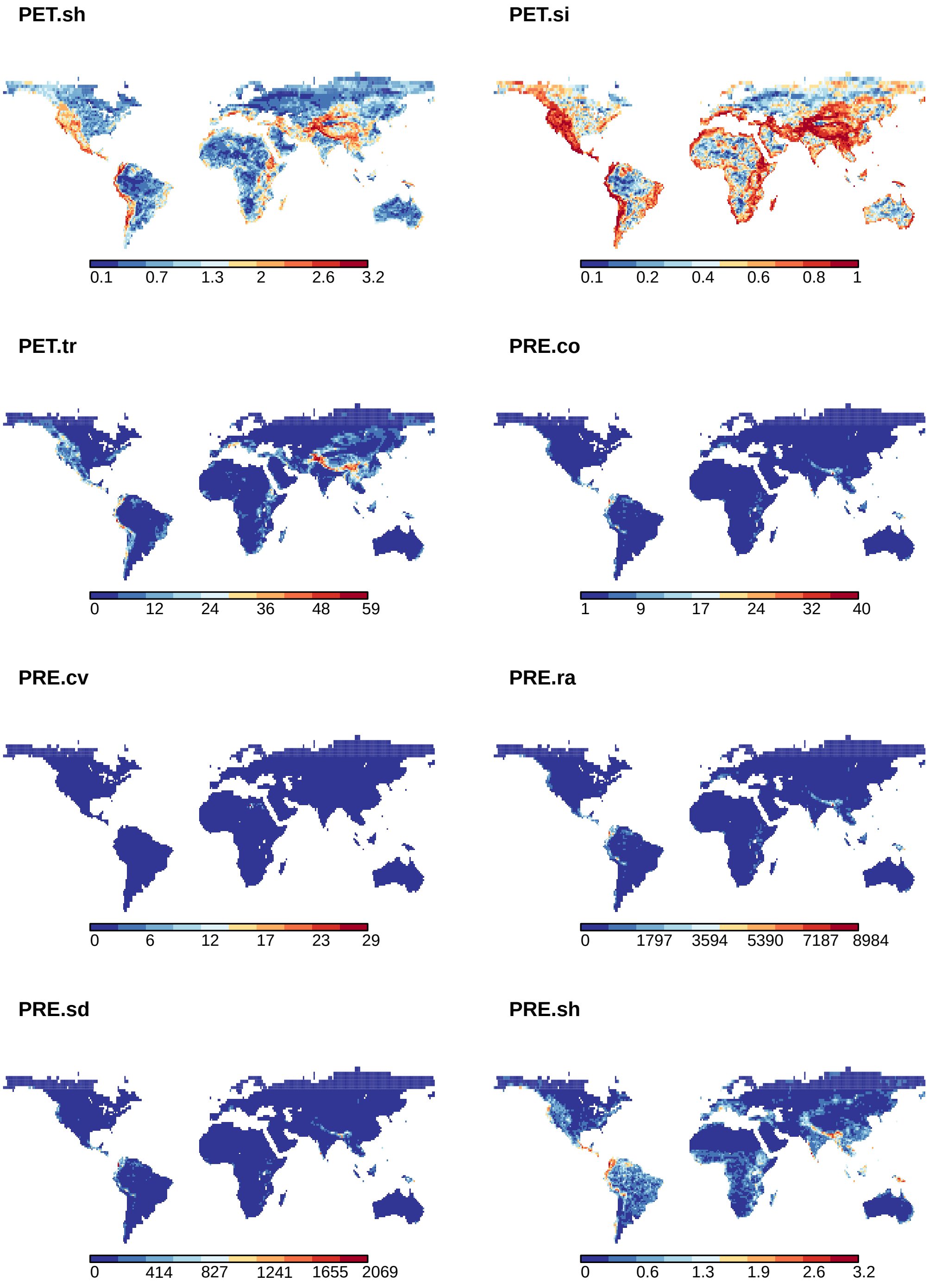
Figure C.4 Maps of EH measures at 111 km × 111 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m^2; PET, mm; PRE, mm; TEM, K; VEG, m.



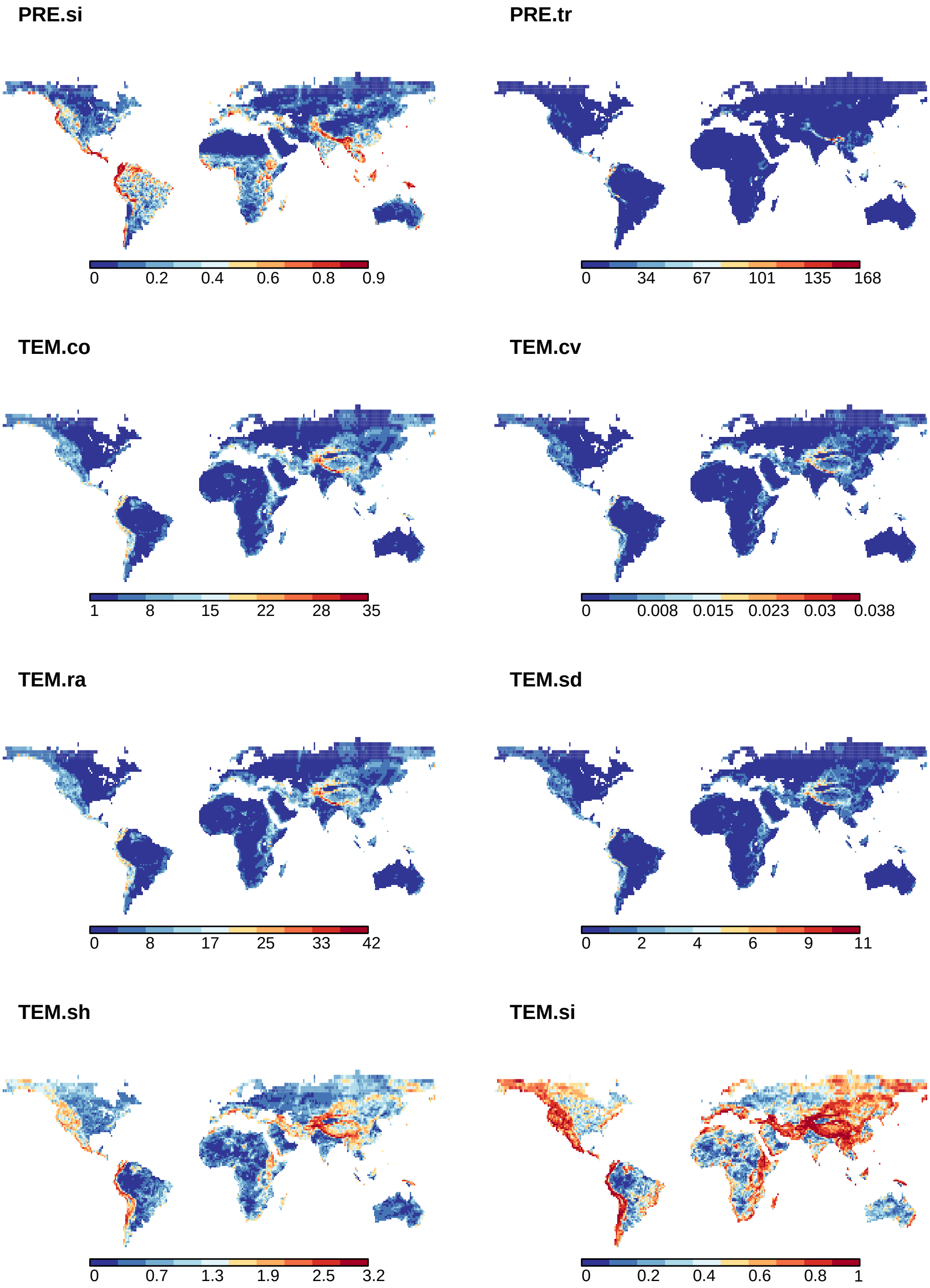
Continued Figure C.4 Maps of EH measures at 111 km × 111 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



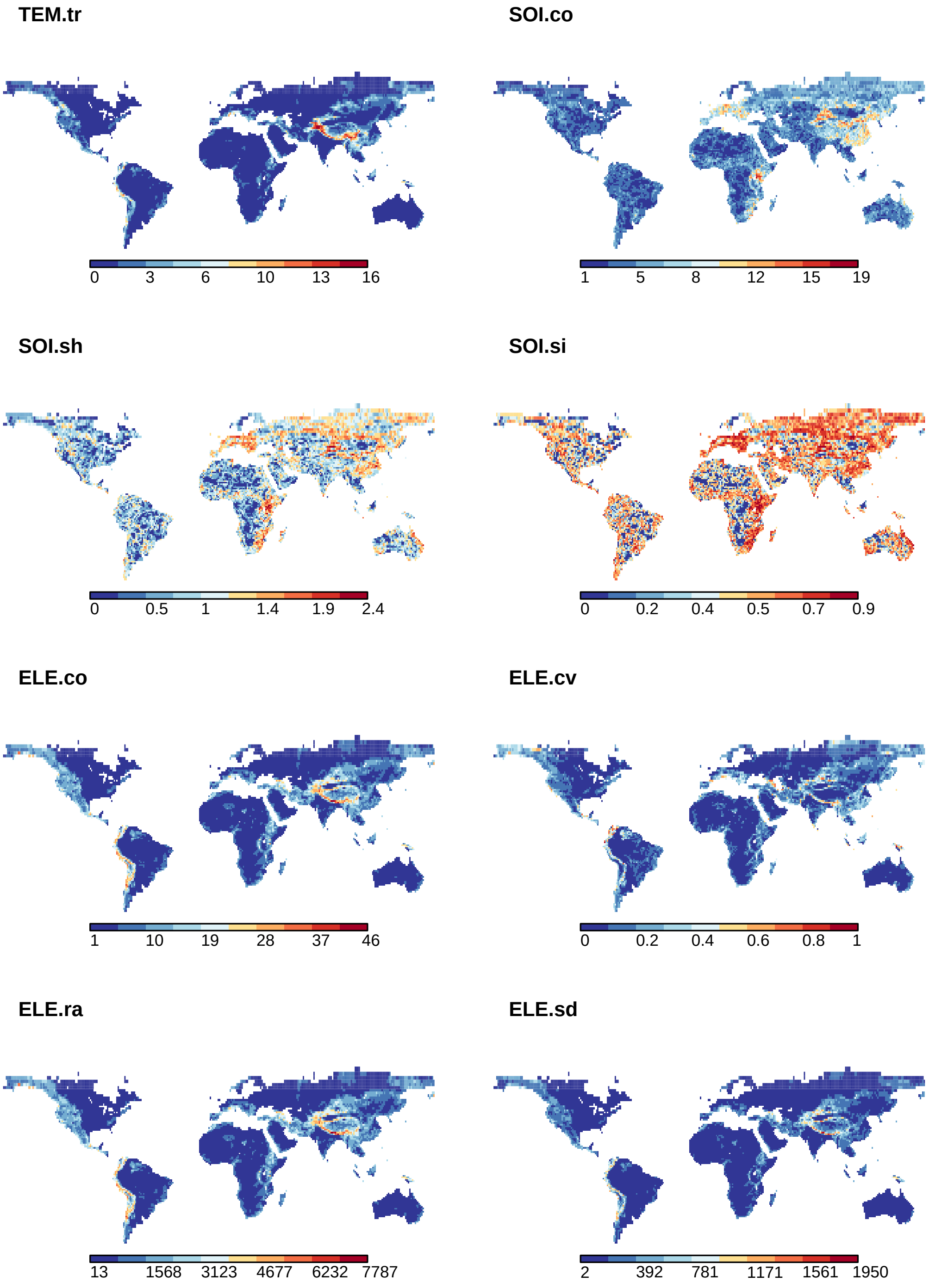
Continued Figure C.4 Maps of EH measures at 111 km × 111 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



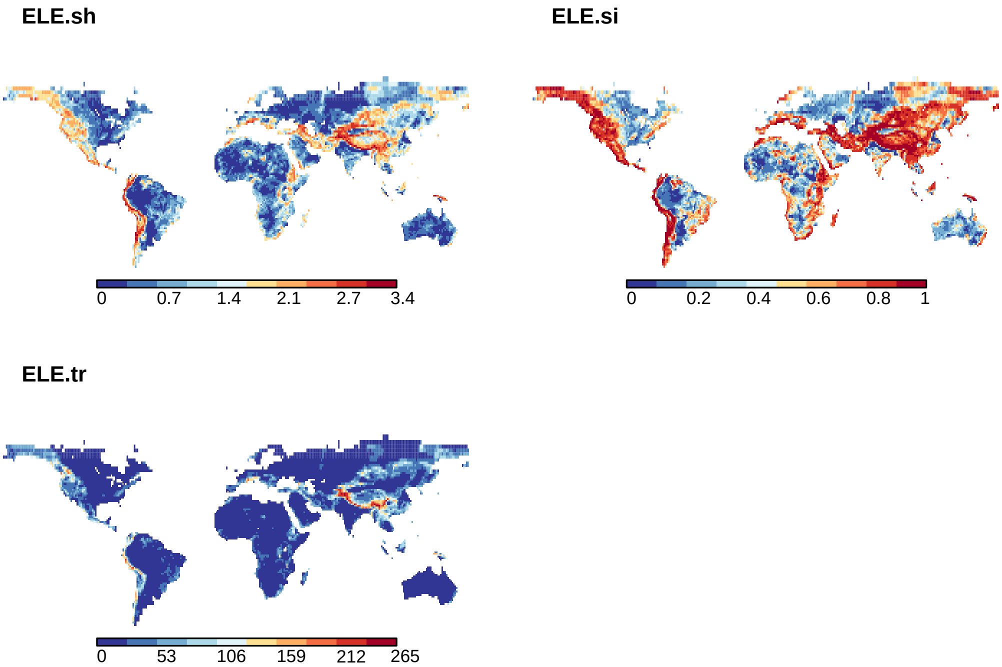
Continued Figure C.4 Maps of EH measures at 111 km × 111 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.4 Maps of EH measures at 111 km × 111 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.4 Maps of EH measures at 111 km × 111 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.4 Maps of EH measures at 111 km × 111 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m^2; PET, mm; PRE, mm; TEM, K; VEG, m.

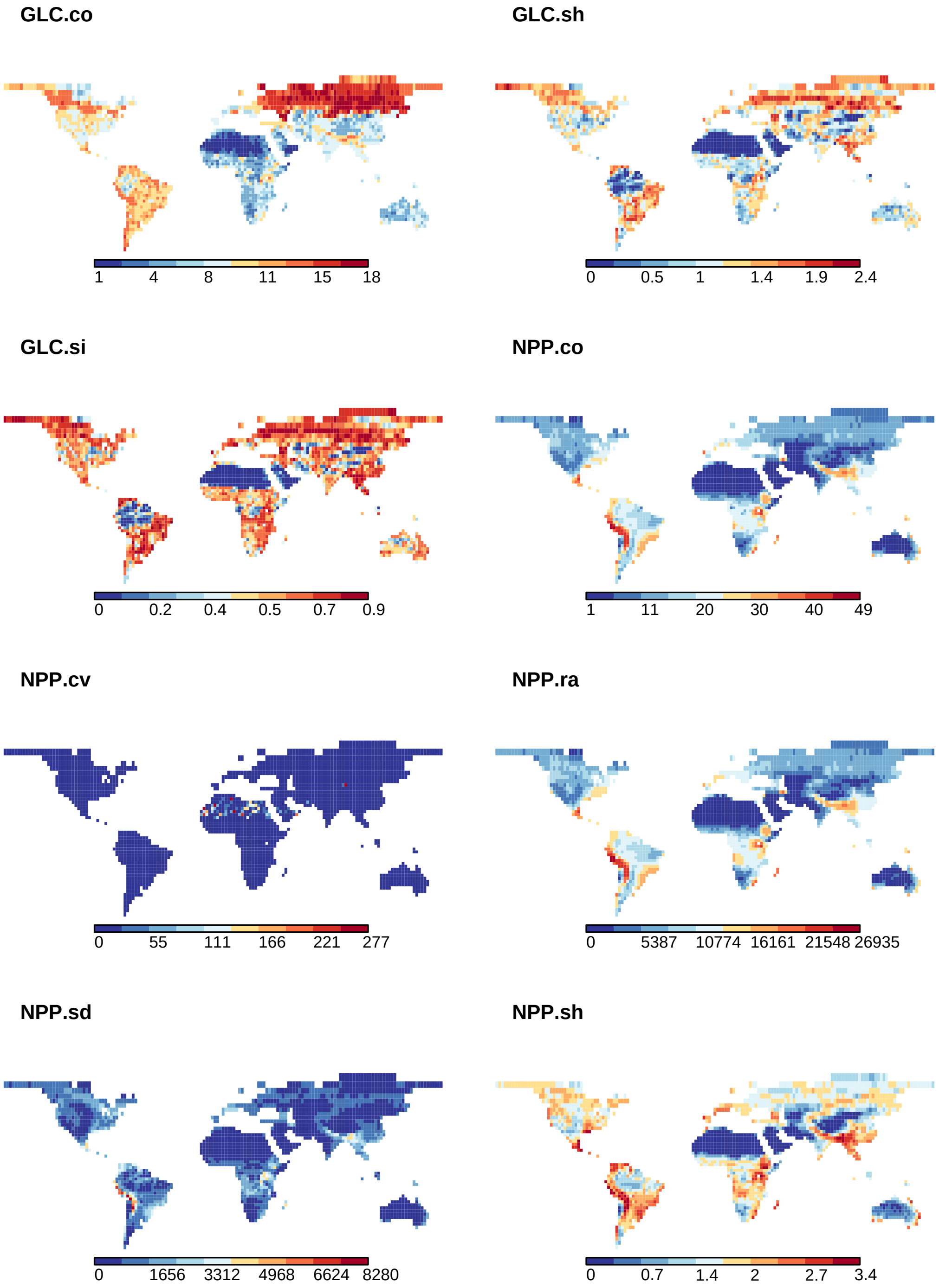
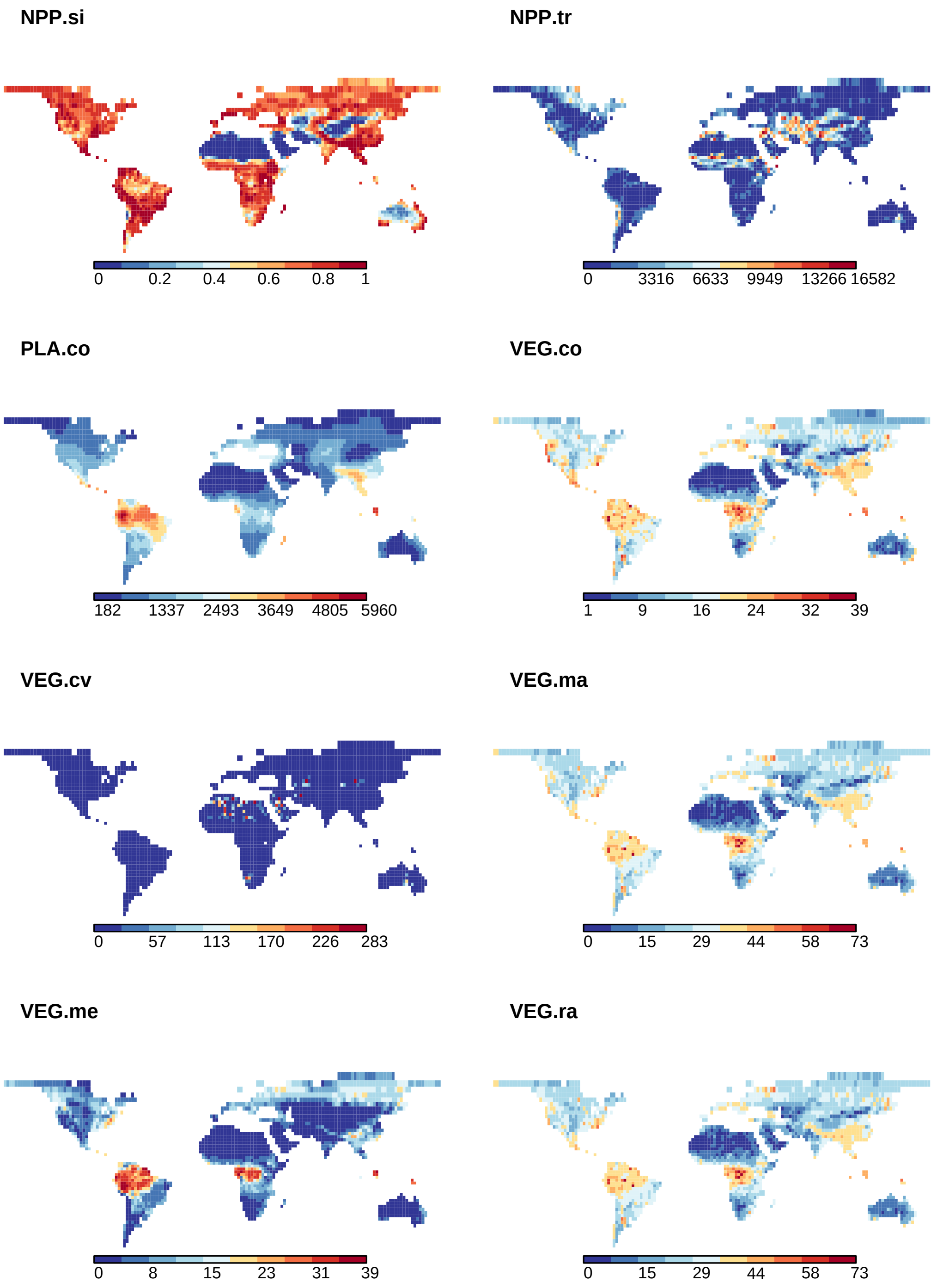
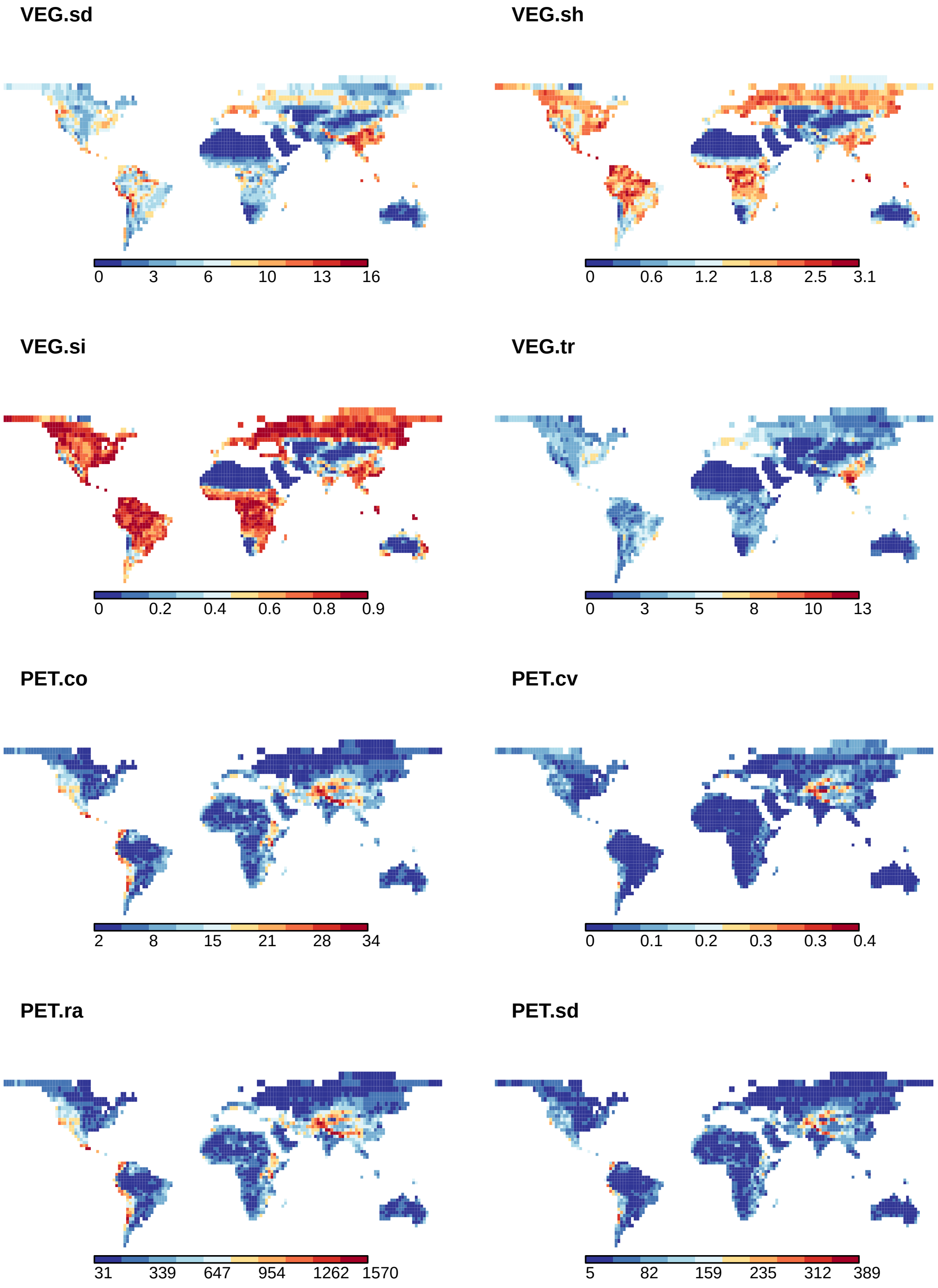


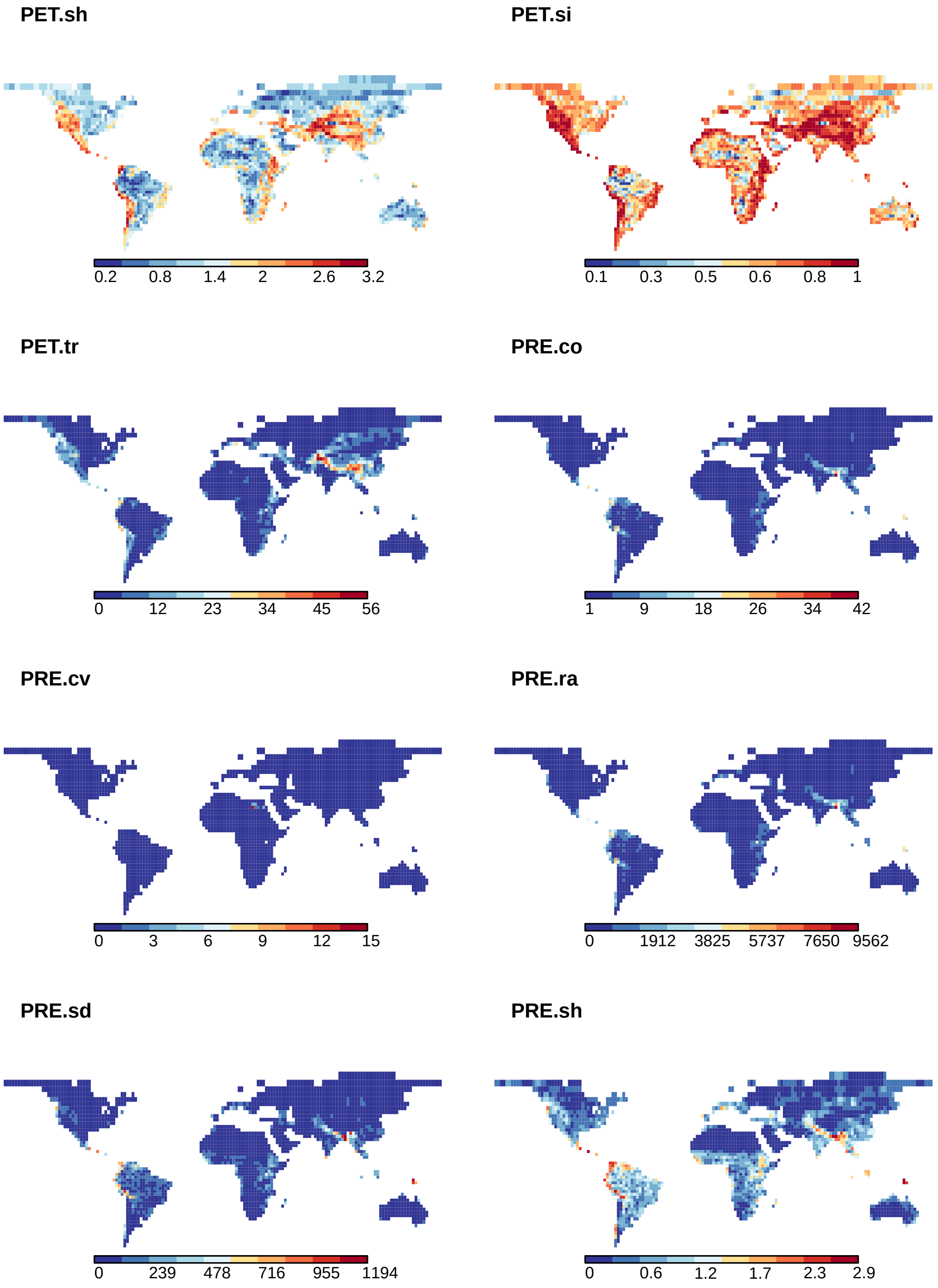
Figure C.5 Maps of EH measures at 222 km × 222 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



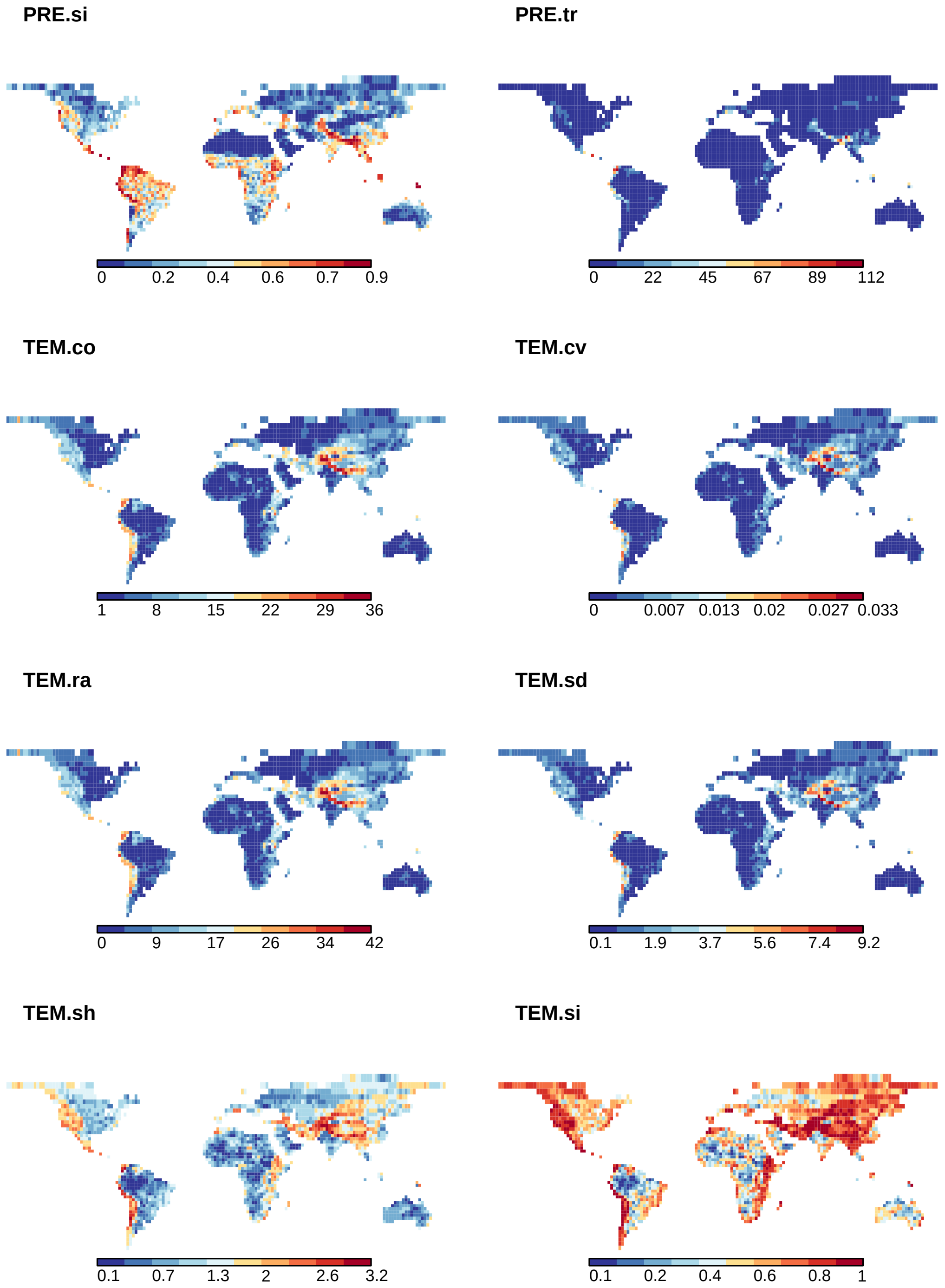
Continued Figure C.5 Maps of EH measures at 222 km × 222 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m^2; PET, mm; PRE, mm; TEM, K; VEG, m.



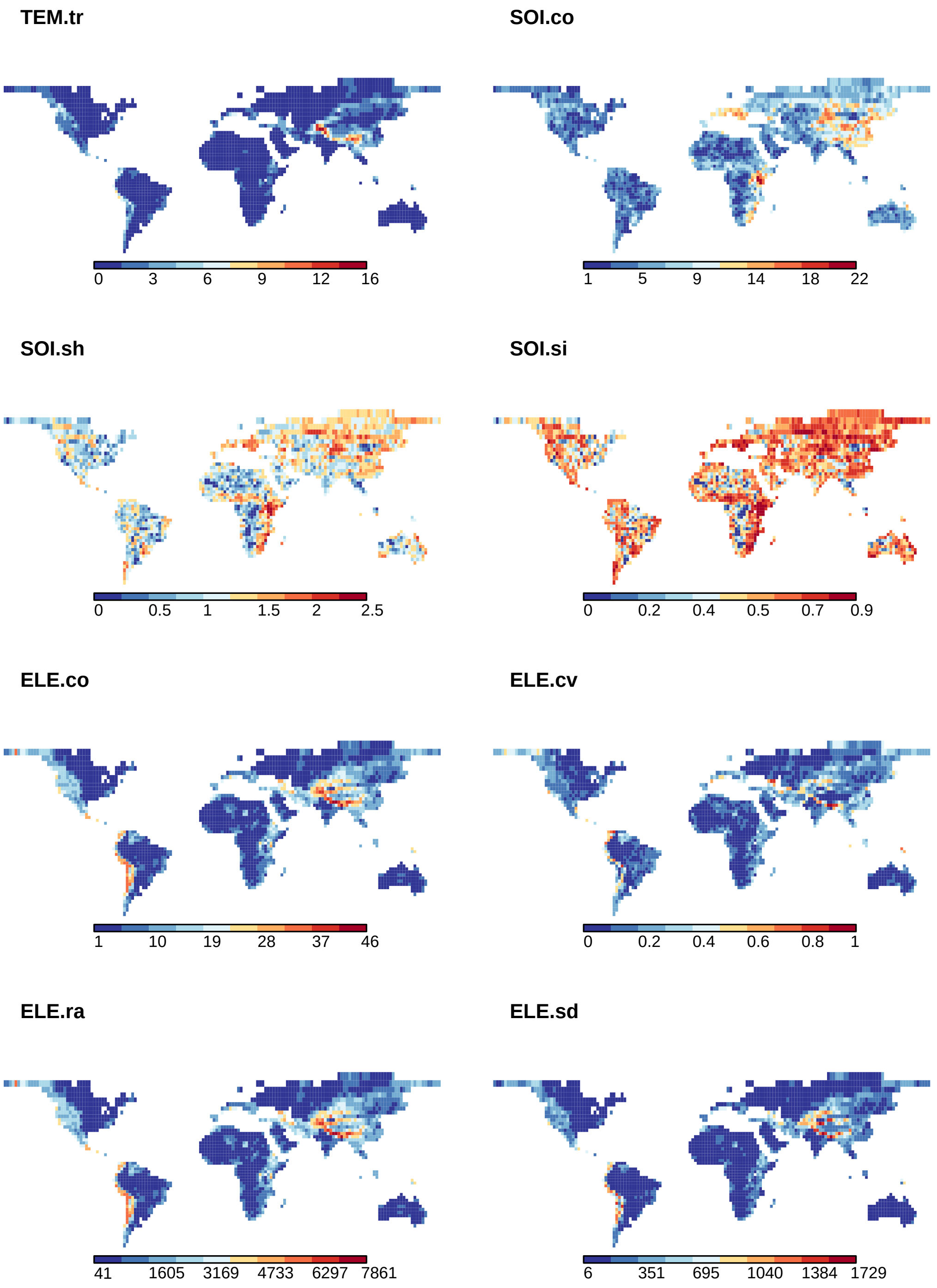
Continued Figure C.5 Maps of EH measures at 222 km × 222 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



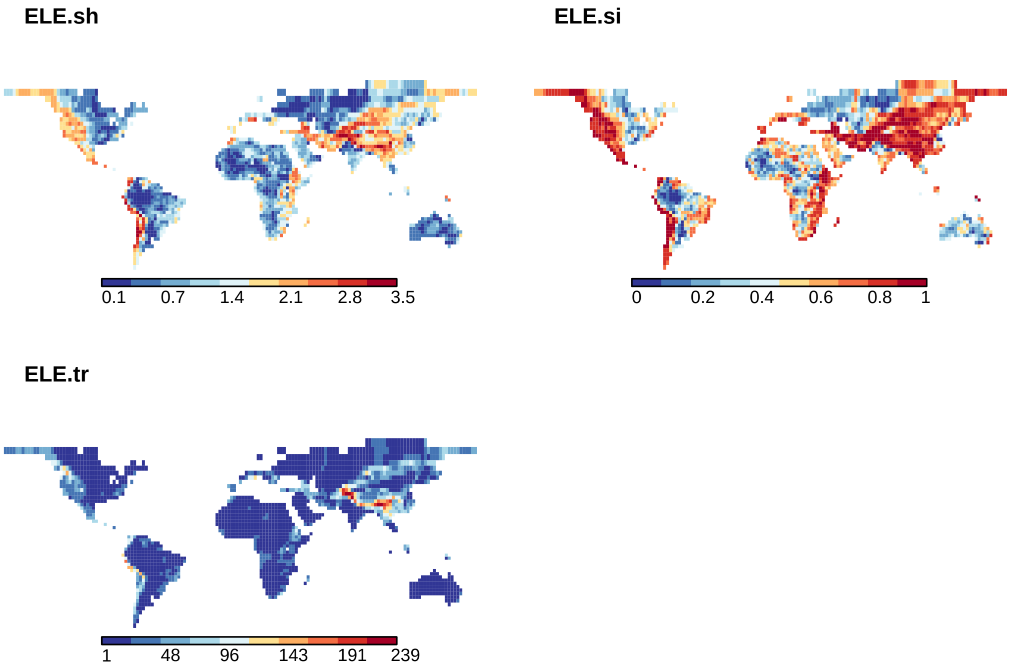
Continued Figure C.5 Maps of EH measures at 222 km × 222 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.5 Maps of EH measures at 222 km × 222 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.5 Maps of EH measures at 222 km × 222 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m^2; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.5 Maps of EH measures at 222 km × 222 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.

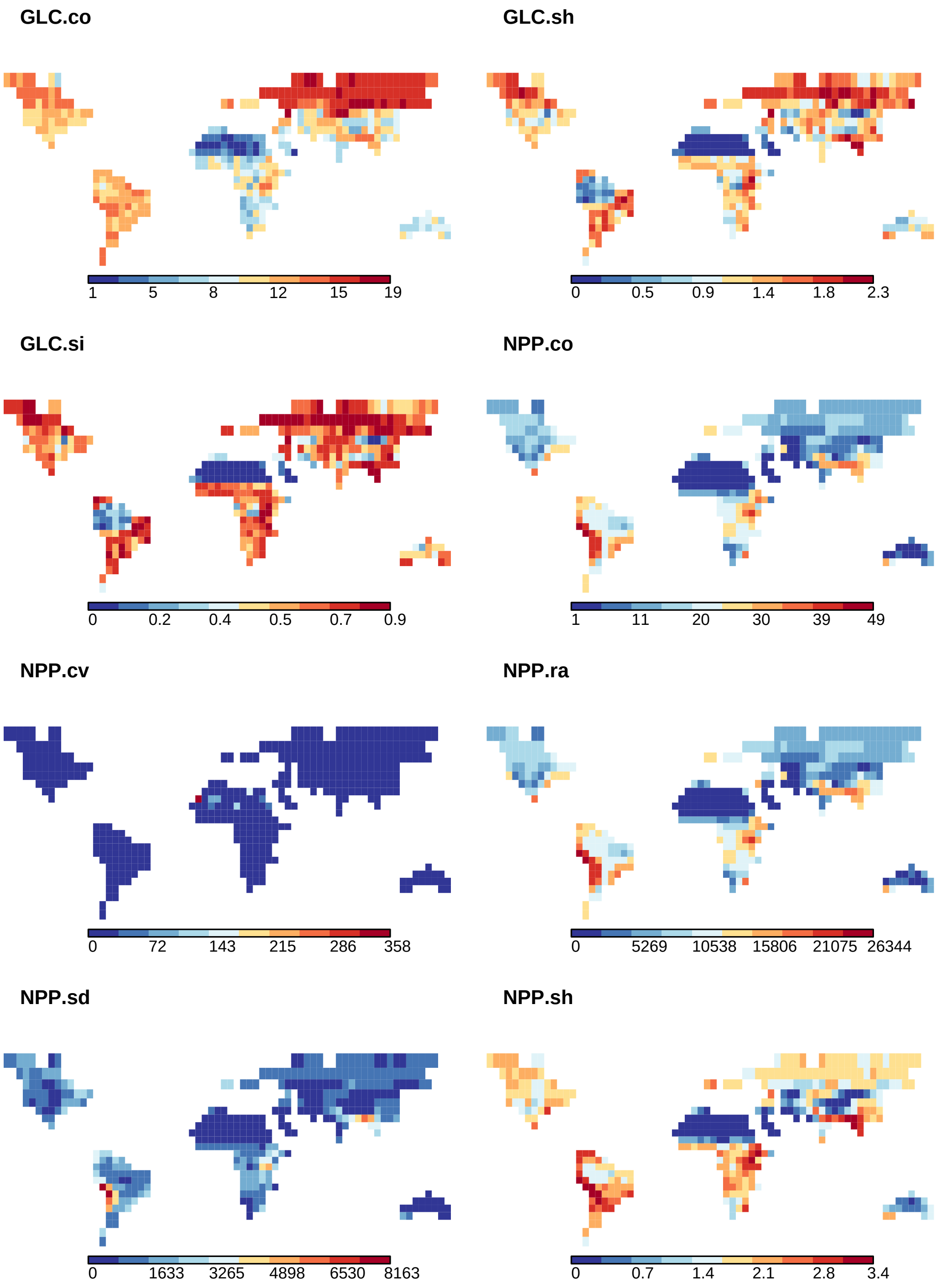
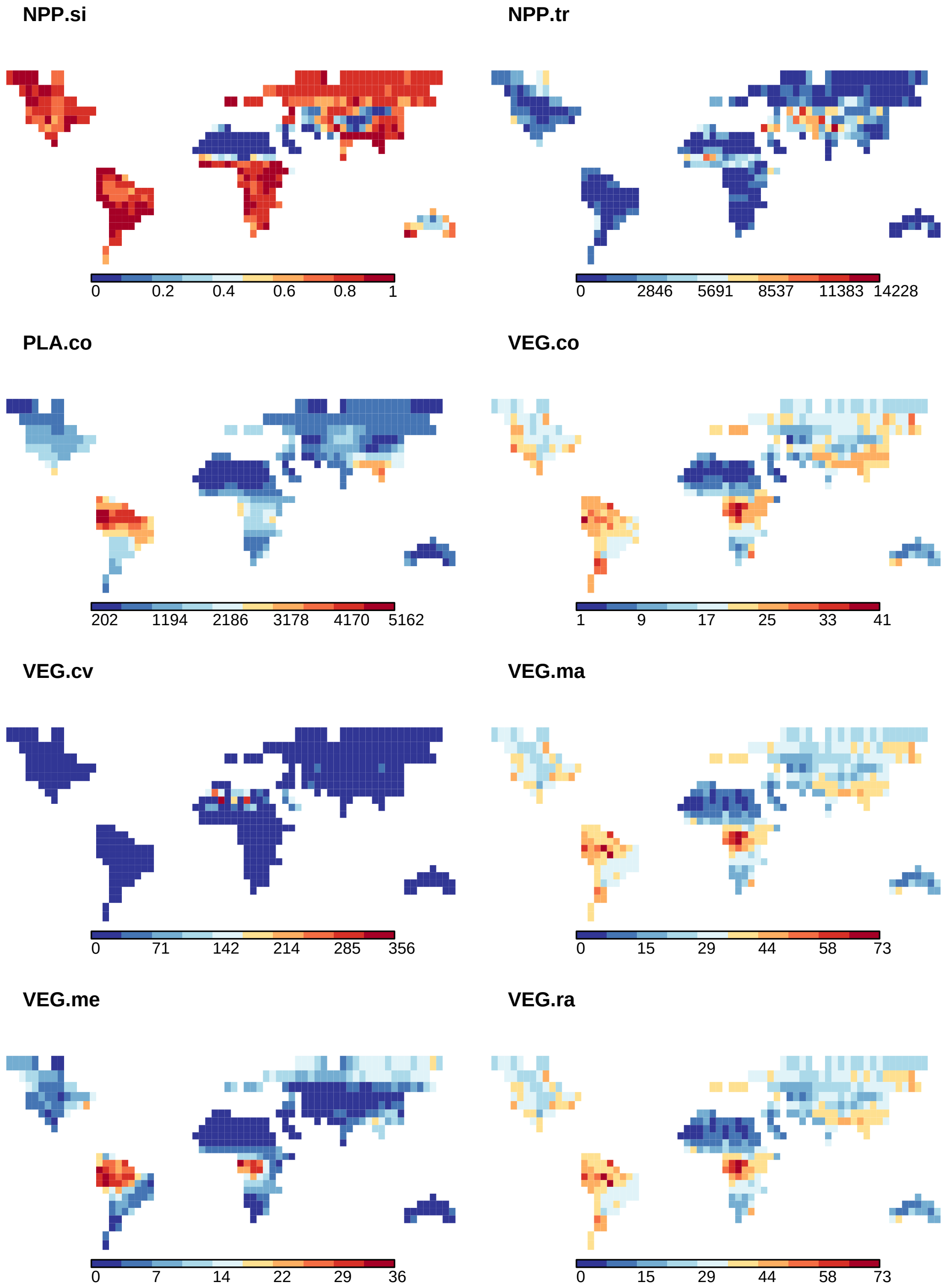
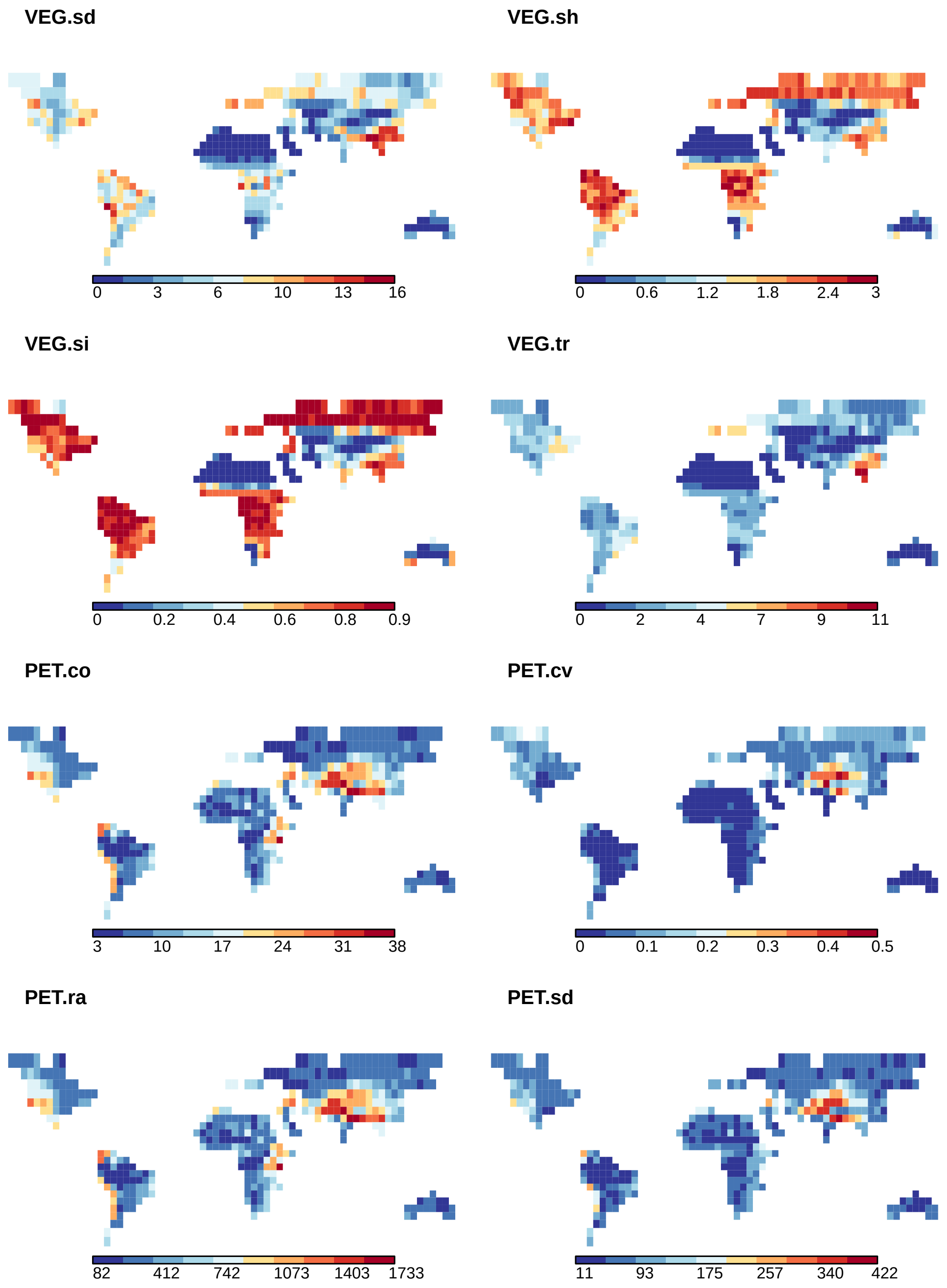


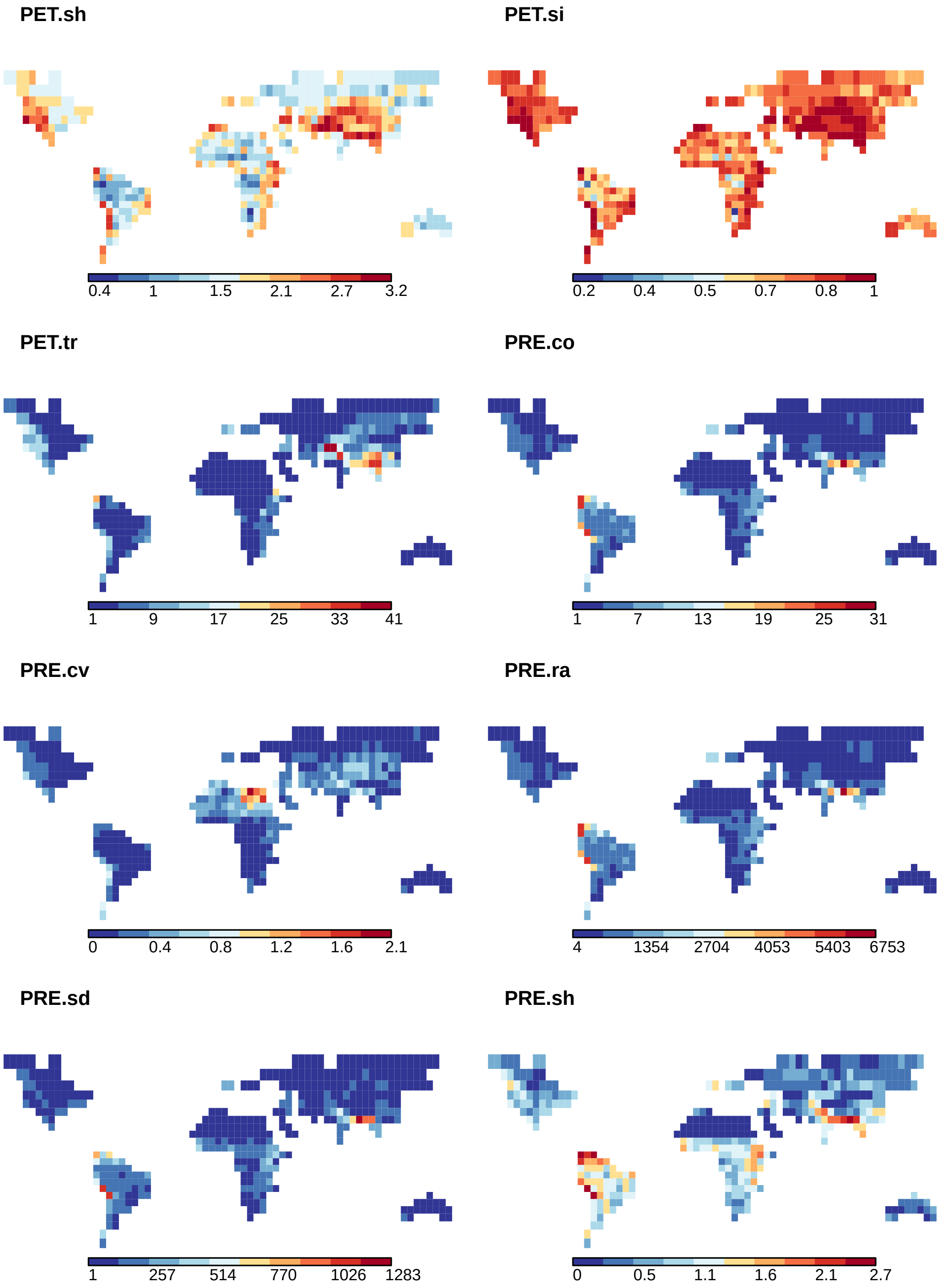
Figure C.6 Maps of EH measures at 444 km × 444 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.6 Maps of EH measures at 444 km × 444 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.6 Maps of EH measures at 444 km × 444 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.


PET.sh

PET.si

PET.tr

PRE.co

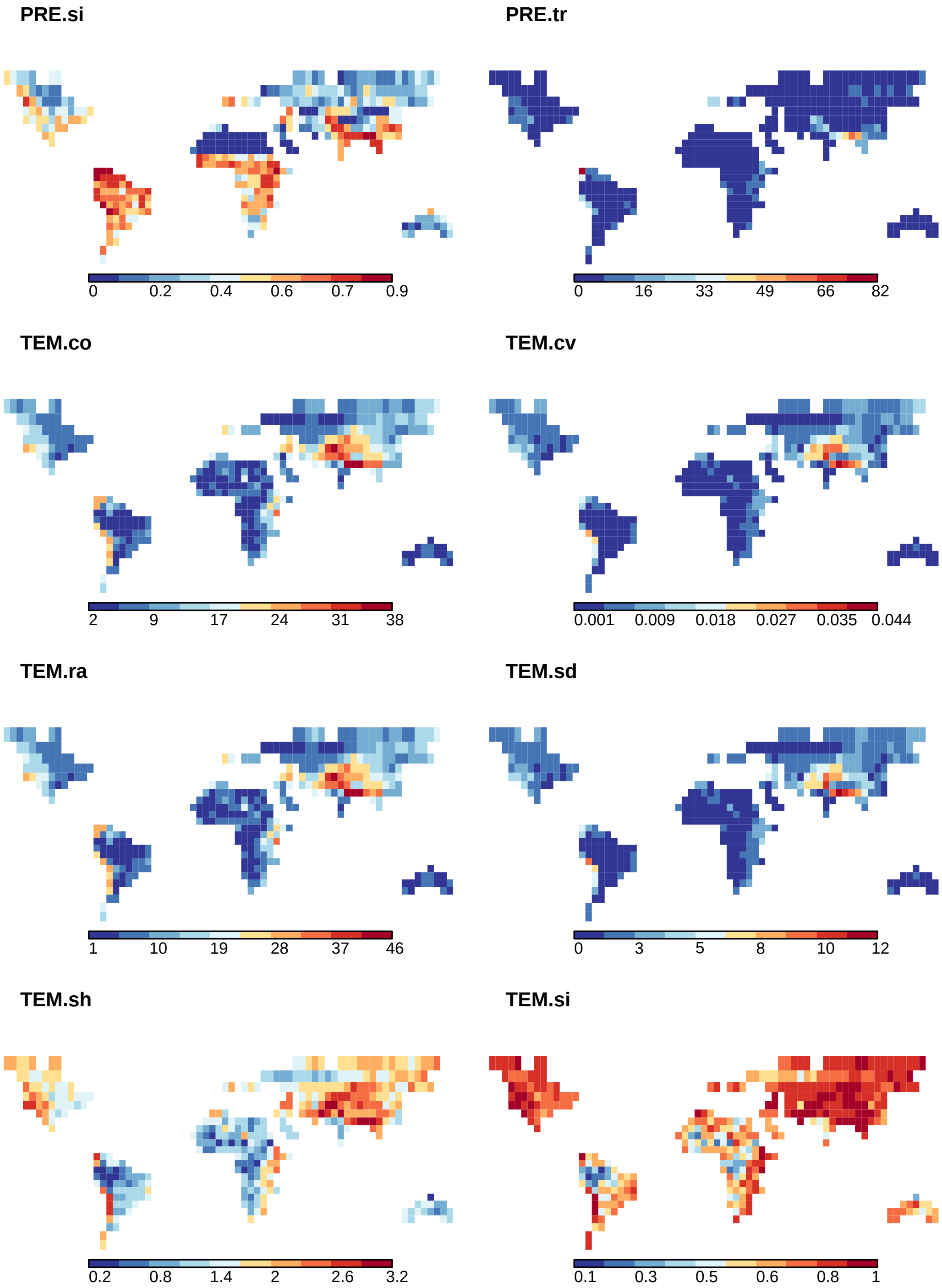
PRE.cv

PRE.ra

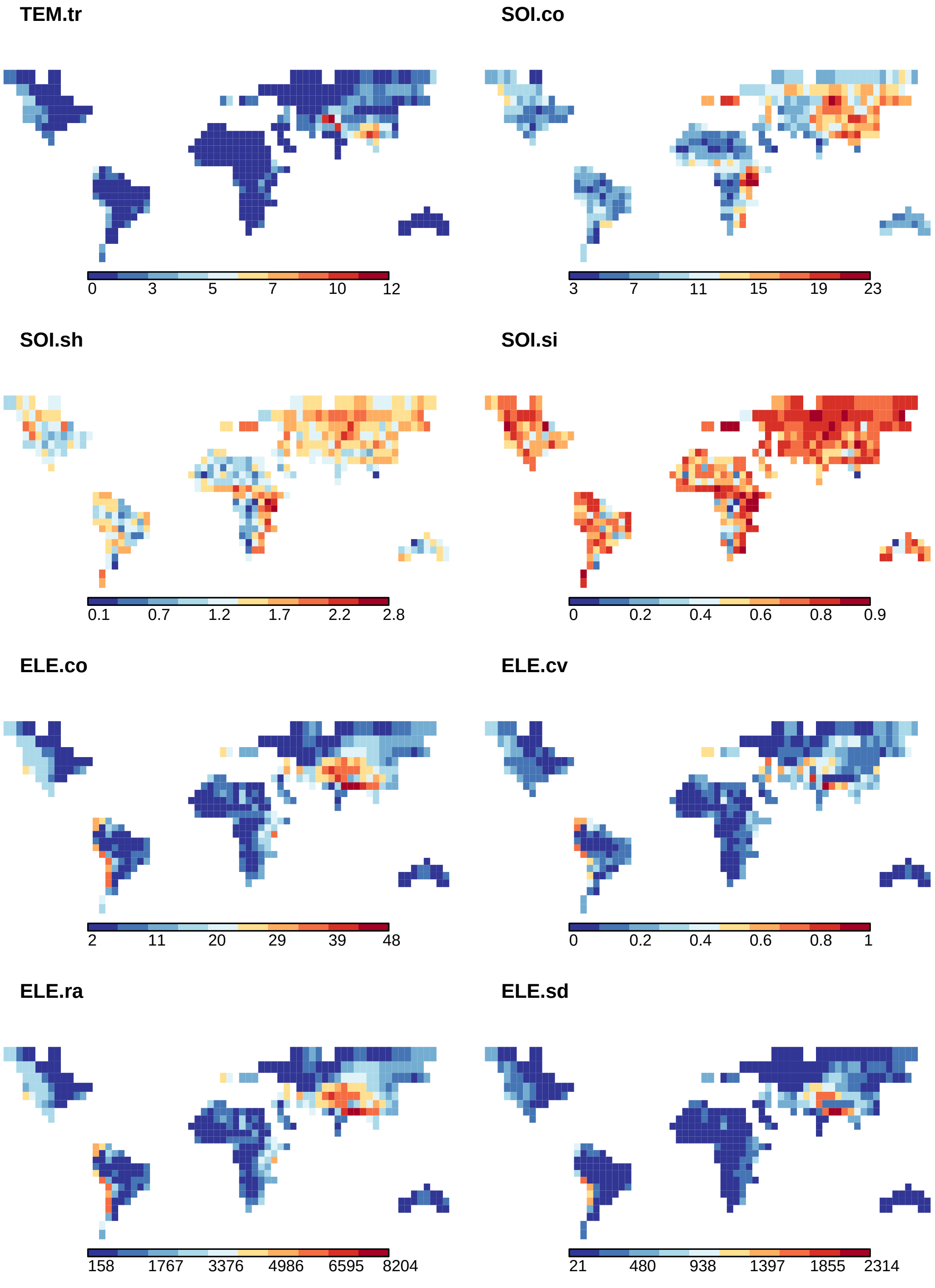
PRE.sd

PRE.sh

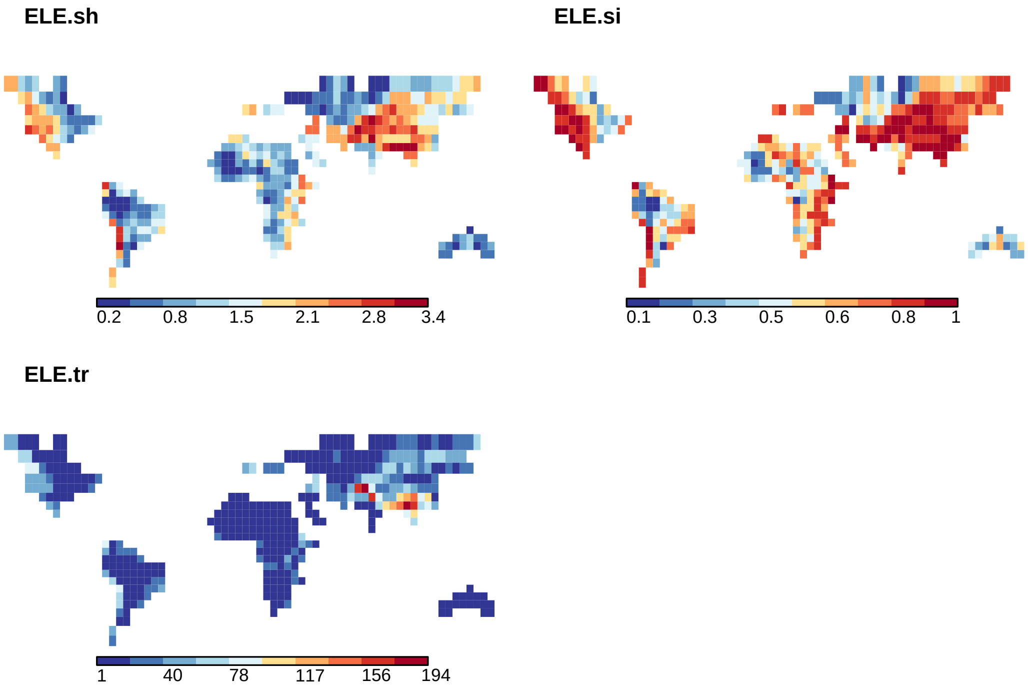
Continued Figure C.6 Maps of EH measures at 444 km × 444 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.6 Maps of EH measures at 444 km × 444 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.6 Maps of EH measures at 444 km × 444 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.



Continued Figure C.6 Maps of EH measures at 444 km × 444 km grain. Coastal cells and large inland water bodies were excluded to derive equal-area study units for the analysis. Colours represent ten equal classes per measure according to the legend. For abbreviations, see Table C.1. Units: ELE, m a.s.l. (values shifted to ≥ 0 by adding the absolute minimum, 431 m); NPP, 0.1 gC/m²; PET, mm; PRE, mm; TEM, K; VEG, m.

C.4 Results from principal component analysis

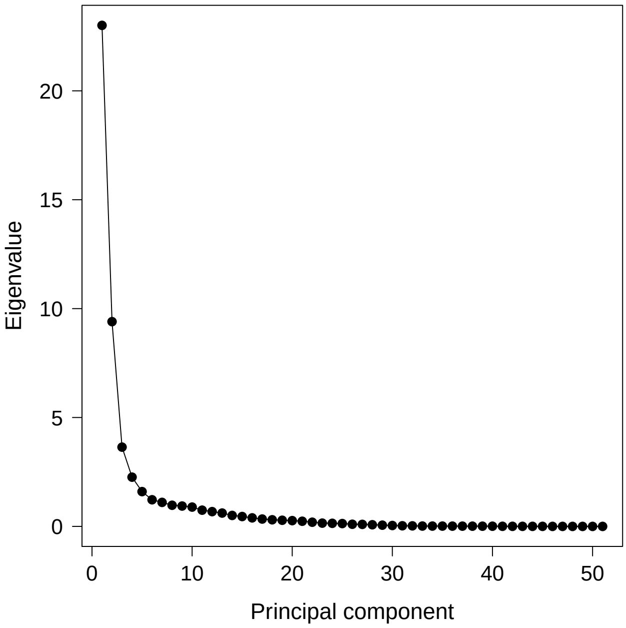


Figure C.7 Scree plot of eigenvalues of principal components from a principal component analysis including 51 EH measures.

Table C.4 Factor loadings for 51 EH measures and eigenvalues of the first three axes from principal component analysis. For abbreviations, see Table C.1.

	PC1	PC2	PC3
GLC.co	0.08	0.14	-0.25
GLC.sh	0.10	0.12	-0.29
GLC.si	0.09	0.12	-0.28
NPP.co	0.13	0.21	0.05
NPP.cv	-0.04	-0.10	0.08
NPP.ra	0.12	0.21	0.05
NPP.sd	0.13	0.16	0.04
NPP.sh	0.13	0.20	-0.09
NPP.si	0.11	0.21	-0.13
NPP.tr	0.03	-0.12	-0.05
PLA.co	0.08	0.17	0.19
VEG.co	0.14	0.21	-0.01
VEG.cv	-0.03	-0.10	0.05
VEG.ma	0.13	0.21	-0.01
VEG.me	0.07	0.21	0.10
VEG.ra	0.13	0.21	-0.01
VEG.sd	0.14	0.19	-0.07
VEG.sh	0.10	0.25	-0.07
VEG.si	0.09	0.25	-0.10
VEG.tr	0.12	0.17	-0.08
PET.co	0.18	-0.13	0.03
PET.cv	0.16	-0.14	-0.09
PET.ra	0.18	-0.13	0.03
PET.sd	0.17	-0.13	0.03
PET.sh	0.17	-0.13	-0.00
PET.si	0.15	-0.12	-0.03
PET.tr	0.17	-0.09	0.03
PRE.co	0.14	0.07	0.28
PRE.cv	0.01	-0.06	0.06
PRE.ra	0.14	0.06	0.28
PRE.sd	0.13	0.06	0.29
PRE.sh	0.15	0.10	0.25
PRE.si	0.15	0.11	0.21
PRE.tr	0.15	0.03	0.23
TEM.co	0.19	-0.13	-0.01
TEM.cv	0.18	-0.13	-0.02
TEM.ra	0.19	-0.13	-0.01
TEM.sd	0.18	-0.13	-0.01
TEM.sh	0.18	-0.13	-0.07
TEM.si	0.16	-0.11	-0.12
TEM.tr	0.17	-0.08	-0.00
SOI.co	0.07	-0.01	-0.26
SOI.sh	0.06	0.00	-0.28
SOI.si	0.05	0.00	-0.26
ELE.co	0.18	-0.12	-0.01
ELE.cv	0.16	-0.05	-0.00
ELE.ra	0.18	-0.12	-0.01
ELE.sd	0.18	-0.12	-0.00
ELE.sh	0.18	-0.12	-0.06
ELE.si	0.16	-0.11	-0.08
ELE.tr	0.18	-0.08	-0.01
Eigenvalue	23.01	9.40	3.64

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