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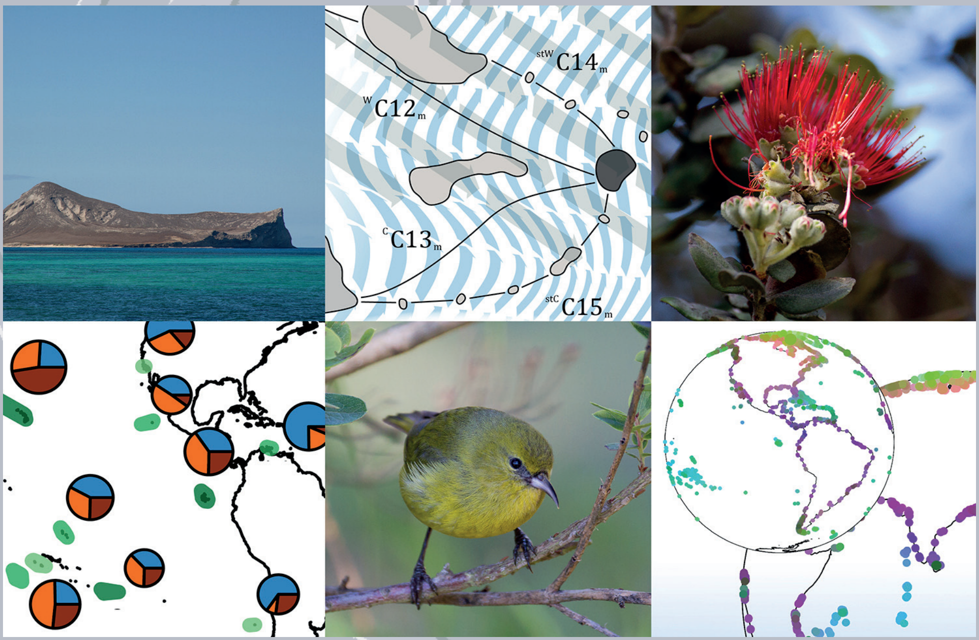
Patrick Weigelt

The Macroecology of Island Floras



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vorgelegt von Patrick Weigelt

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vorgelegt von

M.Sc.

Patrick Weigelt

aus
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We may reveal patterns in the whole that are not evident at all in its separate parts

Robert H. MacArthur
Geographical Ecology, 1972

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Summary

Marine islands harbour a great part of our planet's biological diversity and a high proportion of endemic species. However, island biota are particularly susceptible to anthropogenic threats like climate change, habitat loss and species invasions, making a detailed understanding of ecological processes on islands imperative if we wish to conserve their unique biotas. Due to their discrete and isolated nature, islands are useful model systems in ecological and evolutionary research. So far, however, most studies have concentrated on small-scale biogeographic patterns, and standardized global data on island biogeographic characteristics as well as a macroecological synthesis of their biotas are currently lacking.

In this thesis, I provide a physical and bioclimatic characterization of the world's islands and address the question of how abiotic island characteristics affect the diversity of island floras. I tackle two major aspects of this question: First, I investigate past and present bioclimatic and physical island characteristics as drivers of island plant diversity patterns, focusing on the spatial arrangement of islands and structure of archipelagos. Second, I investigate taxon-specific and trait-related differences in the response of plant diversity patterns to abiotic factors on islands.

I present a database of past and present bioclimatic and physical characteristics including island area, isolation and geology for 17,883 islands larger than 1 km² worldwide. Using ordination and clustering techniques, I characterize and classify the islands in multidimensional environmental space. I also develop a set of ecologically meaningful metrics of island isolation and of the spatial arrangement of islands in archipelagic settings, including metrics related to stepping stones, wind and ocean currents, climatic similarity, inter-island distances and surrounding landmass area. These metrics account for different aspects of island isolation that influence immigration, *in situ* speciation and extinction on islands and turnover among islands. To link abiotic characteristics of islands to biotic attributes of island floras, I use a database of 1,295 island species checklists including c. 45,000 native vascular plant species, compiled for this thesis. It is the first global and most comprehensive dataset on island plant diversity, including species identities instead of mere species numbers.

The global island characterization quantitatively confirms that islands differ from mainland areas in their bioclimatic and physical characteristics. Islands are, on average, significantly cooler, wetter and less seasonal than mainlands. I show that a thorough circumscription of the physical and spatial characteristics of islands and archipelagos, especially isolation, archipelago structure and scale, is needed to understand diversity patterns of their biotas. Isolation is the second most important factor after area determining vascular plant species richness on islands. Among the compared isolation metrics, the proportion of surrounding land area serves best for explaining vascular plant species richness. Also, accounting for stepping stones, large islands as source landmasses and climatic similarity of source areas increases the explanatory power of models compared to considering only the commonly used distance to the nearest mainland. Isolation is less important on large islands where *in situ* diversification counteracts the negative effect of isolation on immigration. At archipelagic scales, the intra-archipelagic spatial structure is particularly important for β diversity, i.e. species turnover among islands, and, indirectly through β, for γ diversity, i.e. the species richness of the entire archipelago. These findings highlight the importance of the spatial location of islands relative to each other for insular diversity patterns and indicate the necessity of considering islands in an archipelagic context in island research and conservation. For ferns on Southeast Asian islands, I show that the importance of physical island characteristics for diversity gradually decreases with spatial grain size from island level to plot level, where local environmental conditions are more important. Local communities may often be saturated, limiting the number of species that can immigrate from the regional species pool. To make predictions about local diversity on islands it is hence important to take the scale-dependence of species pool effects into account.

Major plant groups differ in their dispersal abilities, levels of gene flow, speciation rates and adaptations to climate. Accordingly, comparative analyses among taxonomic plant groups reveal clear differences among taxa in the responses of species richness and phylogenetic diversity patterns to abiotic factors. I find varying island species-area relationships (SPARs), i.e. rates of increase in species richness with island area, among groups. The slope of SPARs is higher in spermatophytes than in pteridophytes and bryophytes, whereas the intercept is lower. In combination, phylogenetic trait and niche conservatism, environmental and dispersal filtering mechanisms and *in situ* speciation are expected lead to phylogenetically clustered assemblages. I show that physical and bioclimatic island attributes, linked to filtering and speciation, influence the phylogenetic structure and diversity of island floras. The strengths and directions of the relationships vary among taxonomic groups. Abiotic predictors explain more variation in phylogenetic diversity and structure for angiosperms and palms than for ferns, which is in accordance with the high dispersal ability and large range sizes of fern species.

The abiotic characterization and regionalization of the world’s islands I present and the accompanying data should facilitate a more integrative consideration of islands in macroecological research. In this thesis, I provide the first predictions of insular vascular plant species richness and analyses of different diversity components (α, β, γ and phylogenetic diversity) of insular systems and their abiotic drivers at a global scale. I show that relationships between environmental drivers and species richness as well as phylogenetic assemblage attributes vary among taxonomic groups in dependence on their predominant dispersal and speciation-related characteristics. This is a new perspective in macroecological island research allowing inferences about the mechanisms underlying patterns of island plant diversity. Furthermore, understanding how the diversity of insular plant groups is shaped by immigration and diversification should promote our understanding of global diversity patterns in general.

Zusammenfassung

Marine Inseln beherbergen einen großen Teil der biologischen Vielfalt unseres Planeten und weisen gleichzeitig einen hohen Anteil endemischer Arten auf. Inselbiota sind allerdings zudem besonders anfällig für anthropogene Einflüsse wie den globalen Klimawandel, Habitatverlust und invasive Arten. Für ihren Erhalt ist es daher wichtig, die ökologischen Prozesse auf Inseln detailliert zu verstehen. Aufgrund ihrer definierten Größe und isolierten Lage eignen sich Inseln als Modellsysteme in der ökologischen und evolutionären Forschung. Der Großteil der bisherigen Inselstudien hat sich allerdings mit kleinräumigen Mustern befasst, so dass standardisierte globale Daten zu den biogeographischen Eigenschaften und eine makroökologische Synthese ihrer Biota bislang fehlen.

In dieser Arbeit stelle ich eine physische und bioklimatische Charakterisierung der Inseln der Welt vor und behandle die Frage, wie abiotische Inseleigenschaften die Diversität von Inselfloren beeinflussen. Ich bearbeite zwei Hauptaspekte dieser Fragestellung: Zuerst konzentriere ich mich auf historische und heutige Klimabedingungen und physische Inseleigenschaften als Triebfedern von Pflanzendiversitätsmustern auf Inseln. Hierbei setze ich einen Schwerpunkt auf die räumliche Anordnung von Inseln und Struktur von Archipelen. Als Zweites behandle ich taxon-spezifische Unterschiede in der Antwort von Diversitätsmustern auf abiotische Faktoren.

Hierzu stelle ich eine globale Datenbank mit historischen und heutigen Klimabedingungen und physischen Eigenschaften, wie Fläche, Isolation und Geologie, von 17883 Inseln größer als 1 km² vor. Mit Hilfe von Ordinations- und Klassifikationsverfahren charakterisiere und klassifiziere ich die Inseln in einem multidimensionalen Umweltraum. Außerdem entwickele ich einen Satz von ökologisch relevanten Maßen zur Beschreibung von Isolation von Inseln und ihrer räumlichen Anordnung in Archipelen, darunter Maße zu Trittstein-Inseln, Wind- und Meeresströmungen, klimatischer Ähnlichkeit, Distanzen zwischen Inseln und umgebender Landfläche. Diese Maße berücksichtigen verschiedene Aspekte von Isolation, welche Immigration, Artbildung und Aussterben auf Inseln sowie Austausch zwischen Inseln beeinflussen. Um abiotische Bedingungen mit biotischen Eigenschaften von Inselfloren in Verbindung zu bringen, nutze ich eine für diese Arbeit erstellte Datenbank aus 1295 Insel-Artenlisten, die insgesamt ca. 45000 heimische Gefäßpflanzenarten umfassen. Dies ist der umfassendste und erste globale Datensatz für Pflanzen auf Inseln, der Artidentitäten anstatt lediglich Artenzahlen beinhaltet.

Die globale Insel-Charakterisierung bestätigt quantitativ, dass sich Inseln in bioklimatischen und physischen Eigenschaften vom Festland unterscheiden. Inseln sind im Durchschnitt signifikant kühler, feuchter und weniger saisonal geprägt als das Festland. Die weiteren Ergebnisse zeigen, dass eine sorgfältige Beschreibung der räumlich-physischen Eigenschaften von Inseln und Archipelen nötig ist, um die Diversitätsmuster ihrer Biota zu verstehen. Isolation ist nach Inselfläche der zweitwichtigste Einflussfaktor für den Gefäßpflanzenartenreichtum auf Inseln. Von den verglichenen Isolationsmaßen eignet sich der Anteil an umgebender Landfläche am besten zur Erklärung der Artenzahlen. Außerdem erhöht sich durch die Berücksichtigung von Trittsteininseln, großen Inseln als Quell-Landflächen und klimatischer Ähnlichkeit der Quell-Landflächen die Vorhersagekraft der Modelle. Isolation spielt eine geringere Rolle auf großen Inseln, wo *in situ* Diversifizierung den negativen Effekt von Isolation auf Immigration ausgleicht. Die räumliche Struktur innerhalb von Archipelen ist von besonderer Bedeutung für β-Diversität, d.h. für den Unterschied in der Artenzusammensetzung der Inseln. Außerdem beeinflusst sie indirekt, durch den Effekt auf die β-Diversität, auch die γ-Diversität, d.h. die Diversität des gesamten Archipels. Die Ergebnisse heben die enorme Bedeutung der relativen räumlichen Position von Inseln zueinander für Diversitätsmuster auf Inseln hervor und zeigen die Notwendigkeit für Inselforschung und Naturschutz, Inseln im Kontext ihres Archipels zu betrachten. Die Ergebnisse für Farne auf südostasiatischen Inseln zeigen, dass die Bedeutung von physischen Inseleigenschaften für Diversität kontinuierlich mit der Größe der betrachteten Untersuchungsfläche von der Insel- bis zur Plotebene abnimmt, wohingegen der Einfluss von lokalen Umweltbedingungen zunimmt. Lokale Artgemeinschaften sind häufig gesättigt, wodurch die Anzahl an Arten, die aus dem regionalen Artenbestand einwandern können, limitiert wird. Um Vorhersagen über lokalen Artenreichtum zu machen, ist es daher wichtig, die Skalenabhängigkeit der Effekte des regionalen Artenbestandes zu berücksichtigen.

Großgruppen von Pflanzen unterscheiden sich in ihrer Ausbreitungsfähigkeit, ihrem Genfluss, Artbildungsraten und Anpassungen an das Klima. Dementsprechend zeigen die vergleichenden Analysen zwischen taxonomischen Pflanzengruppen deutliche Unterschiede in der Reaktion von Artenreichtum und phylogenetischen Diversitätsmustern auf abiotische Faktoren. Die Arten-Fläche-Beziehung, d.h. die Zunahme von Artendiversität mit zunehmender Fläche, variiert zwischen den Pflanzengruppen. Die Steigung der Arten-Fläche-Beziehung ist für Spermatophyten größer als für Pteridophyten und Bryophyten, wohingegen der y-Achsenabschnitt kleiner ist. Unter der Annahme, dass Merkmale und klimatische Anpassungen innerhalb von taxonomischen Gruppen phylogenetisch konserviert sind, führen die Filterwirkung von Ausbreitungsbarrieren und Umwelteigenschaften sowie *in situ* Artbildung zu Gemeinschaften eng verwandter Arten (*phylogenetic clustering*). Die Ergebnisse zeigen, dass physische und bioklimatische Inseleigenschaften, die mit der Filterwirkung und Artbildung in Verbindung stehen, die phylogenetische Struktur von Inselgemeinschaften beeinflussen. Die

Stärke und Richtung der Zusammenhänge variieren zwischen taxonomischen Gruppen. Abiotische Faktoren erklären mehr Variation in phylogenetischer Diversität für alle Angiospermen und Palmen als für Farne, was auf Grund höherer Ausbreitungsfähigkeit und größerer Verbreitungsgebiete von Farnen den Erwartungen entspricht.

Die abiotische Charakterisierung und Klassifizierung der weltweiten Inseln und die zugehörigen Daten ermöglichen eine integrativere Berücksichtigung von Inseln in der makroökologischen Forschung. In dieser Arbeit präsentiere ich die ersten Vorhersagen globaler Pflanzenartenvielfalt auf Inseln und die ersten Analysen zu unterschiedlichen Diversitätskomponenten (α, β, γ und phylogenetische Diversität) von Inselsystemen und ihren abiotischen Einflussfaktoren auf globalem Maßstab. Ich zeige, dass Zusammenhänge zwischen Umweltfaktoren und Artenzahl sowie phylogenetischen Eigenschaften von Inselgemeinschaften zwischen unterschiedlichen taxonomischen Gruppen in Abhängigkeit ihrer vorwiegenden Ausbreitungs- und Artbildungseigenschaften variieren können. Dies ist eine neue Sichtweise in der makroökologischen Inselforschung, die Rückschlüsse auf die Mechanismen hinter Diversitätsmustern von Pflanzen auf Inseln erlaubt. Ein detailliertes Verständnis davon, wie Diversität unterschiedlicher Pflanzengruppen durch Immigration und Diversifizierung auf Inseln entsteht, dürfte auch das Verständnis globaler Diversitätsmuster im Allgemeinen verbessern.

Part I

Introduction

1. Island Biogeography

The question of what determines patterns of biological diversity is one of the main questions in the disciplines of biogeography and macroecology (Brown 1995; Lomolino *et al.* 2010a) and among the 25 most fundamental open questions in science in general (Kennedy & Norman 2005; Pennisi 2005). Past experience suggests that islands may be a key to answering this question.

The biota of isolated islands have attracted interest since the beginning of biogeographic research (e.g. Wallace 1880), and the discrete and isolated nature of islands has fostered some of the most influential theories in ecology, evolution and biogeography (e.g. Darwin 1859; MacArthur & Wilson 1967). The most seminal theory for the field of island biogeography itself was the "equilibrium theory of island biogeography" (ETIB, MacArthur & Wilson 1963, 1967). According to MacArthur and Wilson (1963, 1967), the number of species inhabiting an island arises from a dynamic equilibrium of immigration and extinction. While the immigration rate increases with decreasing degree of island isolation, the extinction rate decreases with increasing island area. MacArthur and Wilson visualized their concept in a famous textbook figure showing immigration rates for isolated and less isolated islands and extinction rates for large and small islands in dependence on species richness of the islands (Fig. I.1.1). The equilibrium state of species richness for a given island is reached where the lines of immigration and extinction cross each other. Robert MacArthur first sketched the graph in 1962 (Lomolino & Brown 2009). Even before that, the PhD student Gordon Munroe (1948) developed a very similar theory of an equilibrium state of species richness on islands depending on rates of immigration, extinction and speciation. He also linked these rates to island area and isolation, however, his thesis did not receive the attention it should have, leading to a close link of the ETIB and MacArthur and Wilson's seminal work in the perception of today's scientists (Brown & Lomolino 1989; Lomolino & Brown 2009).

A principle closely related to the ETIB is "one of community ecology's few laws" (Schoener 1976): the increasing number of species with area, or the species-area relationship (SPAR). The SPAR was first formalized by Arrhenius (1921) and was a basis of MacArthur and Wilson's theory as it predicts a higher number of species on larger islands (Wilson 1961). The SPAR of islands was early recognized as a special case, since on small and isolated islands, rare species are likely to go extinct, whereas on comparable mainland areas, populations can be sustained due to an exchange with adjacent areas (Preston 1962a, b). Species richness on islands hence increases with area more strongly than on mainlands (Rosenzweig & Ziv 1999). SPARs have

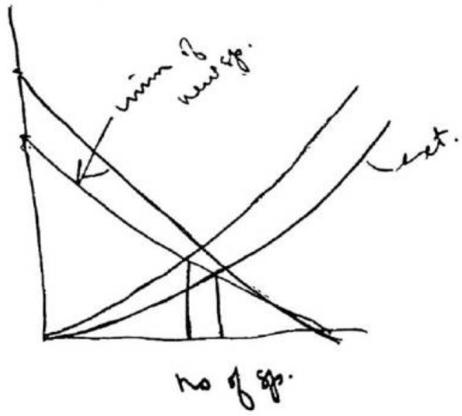

Figure I.1.1. First sketch of the equilibrium model by Robert H. MacArthur from 1962 showing how species richness (“no of sp.”) varies with island area affecting extinction rates (curves labelled “ext.”, upper curve = small island, lower curve = large island) and isolation affecting immigration rates (curves labelled “imm. of new sp.”, upper curve = less isolated island, lower curve = isolated island). Figure simplified from Lomolino & Brown (2009).

been described for a variety of systems (e.g. archipelagic and inter-provincial, Rosenzweig 1995; Rosenzweig & Ziv 1999), and different types of SPARs have been characterized (e.g. nested vs. non-nested settings, Scheiner 2003). Furthermore, the concept has been used to address global patterns in species richness across islands and mainlands (Currie 1991; Kreft & Jetz 2007; Kreft *et al.* 2008), to identify hotspots of species richness (Brooks *et al.* 2002) and to predict extinction under area loss (He & Hubbell 2011; Halley *et al.* 2013). Different formulations of the SPAR and their implications for conservation management (Veech 2000; Guilhaumon *et al.* 2008) as well as its generality among taxa, regions and scales are still under debate (Storch *et al.* 2012; Triantis *et al.* 2012; Aranda *et al.* 2013) (see Chapters II.4 & II.5).

The ETIB highlights island area and isolation as main physical drivers of species richness on islands. Species richness should decrease with island isolation due to decreasing immigration rates (MacArthur & Wilson 1967). However, compared to the area effect, the effect of isolation is difficult to assess and has therefore received less research attention (Whittaker & Fernández-Palacios 2007; Lomolino *et al.* 2010a). Many study systems used to test for the isolation effect exhibited only little variation in isolation and were therefore inept to reveal its importance (Whittaker *et al.* 2001). Quantifying island isolation has proven particularly difficult since isolation is influenced by stepping stone islands (Gilpin 1980), landmass geometry (Taylor 1987), wind and ocean currents (Cook & Crisp 2005) and the amount of surrounding source landmass (Diver 2008) (see Chapter II.2). Especially in archipelagic settings, turnover among islands may affect the diversity of single islands and entire archipelagos (Chiarucci *et al.* 2010) (see Chapter II.3).

Many additions have been made to the ETIB, and its validity has been argued (Sauer 1969). However, its impact on today's understanding of biogeographical patterns and processes is well recognized (Lomolino *et al.* 2010b). Indeed, new research disciplines, such as metapopulation biology (Hanski & Gilpin 1991; Hanski *et al.* 2013), emerged from the ETIB, and it had great impact on landscape ecology, helping to understand the effects of fragmentation and area of habitat patches and protected areas (Diamond 1975; Tilman *et al.* 1994; Gibson *et al.* 2013).

Additions to the ETIB include that also the immigration rate should depend on island area, and also the extinction rate should depend on isolation: Large islands receive more propagules due to a larger target area (“target area effect”, Whitehead & Jones 1969; Gilpin & Diamond 1976), and less isolated islands may receive constant immigration of individuals preventing extinction (“rescue effect”, Brown & Kodric-Brown 1977). Anomalies in the SPARs of small islands (MacArthur & Wilson 1967) due to stochastic processes and idiosyncratic differences among islands, the so-called “small island effect” (Lomolino 2000), led to the development of a more general island SPAR (Lomolino & Weiser 2001). According to Lomolino and Weiser (2001), species richness should show an area-independent response on small islands, a more deterministic response on larger islands, and a second increase of richness with area on islands large enough to provide *in situ* geographic isolation promoting speciation (Lomolino & Weiser 2001). However, in many studies the reported area-independence of species richness on small islands may be due to inappropriate statistical methods (Dengler 2010).

Depending on the temporal and spatial scale of analysis, different factors additional to area and isolation are important for shaping island diversity patterns (Whittaker *et al.* 2001). Island area itself has no direct effect on the organisms inhabiting an island, but it is a surrogate for two factors (MacArthur & Wilson 1967; Wright 1983): first, larger islands provide a greater amount of resources and may therefore hold larger populations; second, larger islands provide larger habitat diversity, supporting a greater variety of species. Both effects may be addressed more directly. The amount of resources, or available energy, depends on macro-climatic conditions. At large spatial scales where climate shows substantial variability, climatic variables representing available energy should hence affect extinction and species richness on islands ("species-energy theory", Wright 1983; Kreft *et al.* 2008). Accordingly, habitat diversity may be addressed more directly by measures of environmental heterogeneity, e.g. the number of habitat types, and incorporated into island biogeographical models ("choros model", Triantis *et al.* 2003; Kreft *et al.* 2008; Hortal *et al.* 2009).

Already MacArthur and Wilson (1967) and Munroe (1948) highlighted the importance of evolution on islands for the composition and size of island biotas. Recent conceptual models rigorously incorporated evolutionary processes into the framework of island biogeographic theory. Oceanic islands are geologically relatively ephemeral, emerging from the ocean and submerging again after several million years (Whittaker & Fernández-Palacios 2007). Their carrying capacity changes over time and so do immigration, extinction and speciation rates as well as the realized species richness ("general dynamic model", Whittaker *et al.* 2008; see also Steinbauer *et al.* 2013). Speciation on islands also depends on the above discussed island characteristics isolation, area and environmental heterogeneity. As the rate of gene flow decreases with increasing isolation, speciation on islands should be more important on more isolated islands (Heaney 2000; Kisel & Barraclough 2010). *In situ* diversification or cladogenesis is more likely on large and heterogeneous islands that support *in situ* reproductive isolation (Losos & Schluter 2000; Stuessy *et al.* 2006; Stuessy & Ono 2007; Kisel & Barraclough 2010). The degree of endemism should hence increase with isolation and area (Mayr & Diamond 2001).

Both limited colonization and evolutionary processes on isolated islands contribute to the uniqueness of island biotas (Mayr & Diamond 2001; Losos & Ricklefs 2009). Species differ in their abilities to colonize islands and to persist and evolve on islands, leading to disharmonic island assemblages compared to mainlands (Carlquist 1967; Gillespie & Roderick 2002) (see Chapters II.5 & II.6). Only species adapted to long-distance dispersal reach isolated islands (Wilson 1959; Gillespie *et al.* 2012). Similarly, albeit less easy to link to species characteristics, extinction may act as a filter, favouring species that require less energy to maintain their populations on small islands (Brown 1981). Communities on small and species poor islands hence tend to be non-random, nested subsets of mainland or larger island communities (Wright *et al.* 1997). However, on islands large enough to promote speciation, the disharmonic nature of island assemblages may be largely driven by *in situ* diversification and especially by radiations (Gillespie & Roderick 2002).

Islands, especially oceanic archipelagos implying inter-island reproductive isolation, have been arenas of iconic adaptive radiations (Losos & Ricklefs 2009). In classic examples like Darwin's finches (15 species on the Galapagos islands, Grant 1998; Grant 2001) or the Hawaiian silversword alliance (30 spp., Losos & Ricklefs 2009; Givnish 2010), descendents of single species diversified into a variety of species supported by the early availability of niche-space on oceanic archipelagos (Losos & Ricklefs 2009). Allopatric speciation and subsequent re-colonization into sympatry led to natural selection favouring character displacement. Radiations most strikingly occur in groups with short generation times, high reproductive rates and high mutation rates (Brookfield 2009; e.g. c. 500 species of Hawaiian Drosophila, Losos & Ricklefs 2009).

In contrast to cladogenesis on isolated, large and heterogeneous islands and archipelagos, anagenesis, i.e. divergence of a species from its mainland ancestor through time without further diversification, is important on islands with low environmental heterogeneity (Stuessy *et al.* 2006) and islands of intermediate degree of isolation (Rosindell & Phillimore 2011). Populations on oceanic islands are usually founded by only a few immigrating individuals ("founder event") and may be subjected to stochastic catastrophic disturbances like volcanic eruptions or hurricanes leading to population bottlenecks. Genetic drift, i.e. randomly changing allele frequencies, may have strong effects on such small populations, paving the way for speciation ("founder effect", Carson & Templeton 1984). Subsequent selection and reproductive isolation from source populations may lead to anagenetic speciation (Stuessy *et al.* 2006).

Evolution on islands is characterized by selective pressures dramatically shifted compared to those present in mainland environments, leading to interesting phenomena or so-called “island syndromes”, like flightlessness in birds and insects or the loss of long-distance dispersal ability and defence mechanisms against herbivory in plants (Grant 1998; Whittaker & Fernández-Palacios 2007). These phenomena can be explained by ecological release from predators and competitors or by the selective disadvantage of certain traits on insular systems surrounded by open water (e.g. long-distance dispersal; Carlquist 1974). The most prominent pattern is the trend of small species to become larger and of large species to become smaller on islands, which is most dominant in mammals ("island rule", van Valen 1973; Heaney 1978; Lomolino 1985; but see Meiri *et al.* 2005). Competitive release in small species and resource limitation in large species are considered the most important reasons for the general pattern (Lomolino 1985). The complementary phenomenon in plants is the development of woodiness and gigantism in otherwise herbaceous angiosperms (e.g. tree sunflowers on Galápagos). One possible explanation among others (see, e.g., Carlquist 1974), following the rationale of the taxon cycle theory by Wilson (1959; 1961), is that evolution of woodiness on islands is associated with shifts from herbaceous species from open early successional habitats into woody species that occupy a niche, on the mainland occupied by poorly dispersing trees (Givnish 1998). In plants, island syndromes also include adaptations to the lack of symbionts possibly leading to the loss of flower attractiveness and shifts to wind-pollination or adaptations to unusual pollinators or dispersers (Whittaker & Fernández-Palacios 2007).

The peculiarities of island biotas, like their depauperate and disharmonic nature and their obvious examples of adaptive evolution, and the small size, distinct boundaries, the relative youth and geographic isolation of islands have rendered them model systems in evolutionary and biogeographic research (Losos & Ricklefs 2009). Research on island systems helped to understand basic patterns and processes underlying species richness, community assembly, and evolution. However, island research was mainly restricted to certain model archipelagos (but see, e.g., Meiri *et al.* 2005; Kalmar & Currie 2006; Kreft *et al.* 2008; Novosolov & Meiri 2013). Global macroecological island analyses may help to deepen our understanding of processes shaping broad-scale patterns of biodiversity which come to light on islands more obviously than anywhere else.

2. Macroecological island research

Macroecology is a large scale, multi-species approach to investigating the diversity, assembly and structure of biotas (Brown & Maurer 1989; Brown 1995; Gaston & Blackburn 2000; Beck *et al.* 2012). In contrast to classic ecology, experimental manipulations at spatial scales appropriate for studying species distributions are infeasible (Brown & Maurer 1989; Brown 1995). Macroecology therefore tries to identify general patterns and to understand processes that determine the diversity, abundance, and distribution of organisms (Brown & Maurer 1989) by applying statistical models to biotic and abiotic variables across spatial and temporal scales and among large numbers of ecological replicates (Brown & Maurer 1989; Brown 1995). Focus of analyses may, e.g., be individuals, species, communities, or assemblages of sample areas like islands (Lomolino *et al.* 2010a).

Many early and influential macroecological studies focused on biogeographic patterns of body size, range size and abundance in vertebrates (Brown & Maurer 1989; Gaston 1990; Brown 1995; Gaston 1996b, a; Gaston & Blackburn 1996). However, the field has expanded greatly during the last decades, including a focus on global diversity gradients (Ceballos & Ehrlich 2006; Hawkins *et al.* 2007; Kreft & Jetz 2007). This was made possible by the increasing availability of biotic and abiotic data at increasing spatial resolution (Jetz *et al.* 2012a) and increased computational possibilities due to modern computers and powerful open source statistical software (R Development Core Team 2010). Especially in terrestrial vertebrates, the availability of species range maps triggered research progress (e.g. IUCN 2008). In plants, which are about ten times as species-rich, global range maps are available at family level only (e.g. Stevens 2001). However, the increasing amount of point collection data (e.g. the Global Biodiversity Information Facility, www.gbif.org), vegetation plots (e.g. the Global Index of Vegetation-Plot Databases, www.givd.info), efforts made towards regional botanical syntheses (e.g. the Botanical Information and Ecology Network (BIEN), bien.nceas.ucsb.edu/bien/) and the large number of regional checklists and floras (Frodin 2001) open up avenues for rigorous large scale analyses.

Currently, macroecology is advancing by considering the evolutionary history of species and their phylogenetic relationships (e.g. Davies & Buckley 2012; Fritz & Rahbek 2012; Kissling *et al.* 2012b; Hawkins *et al.* 2013) as well as functional similarity among species (e.g. Safi *et al.* 2011; Ricklefs 2012), triggered by the deciphering and computing of comprehensive phylogenies and the development of large trait databases (e.g. TRY for plants, Kattge *et al.* 2011). Dated and un-dated species level phylogenies are available, e.g., for major vertebrate clades (Bininda-Emonds *et al.* 2007; Fritz & Rahbek 2012; Jetz *et al.* 2012b) and genus to family level phylogenies for major plant groups (Davies *et al.* 2004a; Baker *et al.* 2009; Bell *et al.* 2010; Lehtonen 2011).

The first example that James Brown uses in his book on macroecology (1995) deals with insular systems, i.e. with extinction risk of small mammal species on isolated mountain tops due to climate change (McDonald & Brown 1992). Also, some of the classic island biogeographic concepts were already empirically tested in a macroecological way according to the definition above. Preston (1962a, b) as well as MacArthur and Wilson (1963, 1967), e.g., used literature data on the species richness of breeding birds in the Caribbean islands and the Southeast Asian islands respectively, to deduce the island SPAR. However, truly global macroecological analyses of island systems are rare. This is surprising considering the well-appreciated suitability of islands as model systems in natural experiments of ecology and evolution (Losos & Ricklefs 2009). The analysis of macroecological patterns of insular diversity may help to understand drivers and processes shaping global diversity patterns, such as speciation and extinction as well as immigration and establishment.

Islands are usually not excluded in general from global macroecological studies. However, due to coarse spatial grains applied in most studies and the small size of most islands, only few very large islands are commonly represented. Nevertheless, peculiarities of islands like outstandingly high endemism or phylogenetic clustering have been noted (Kier *et al.* 2009; Fritz & Rahbek 2012; Kissling *et al.* 2012b). Global scale macroecological island studies include investigations on drivers of species richness (Kalmar & Currie 2006; Kreft *et al.* 2008; Hortal *et al.* 2009) and studies specifically addressing the SPAR (Santos *et al.* 2010b; Triantis *et al.* 2012). Few large scale studies go beyond species richness as a response variable, e.g. addressing species turnover (Stuart *et al.* 2012), invasive species and biotic homogenization (Kueffer *et al.* 2010; Shaw *et al.* 2010), speciation (Kisel & Barraclough 2010; Patiño *et al.* 2013a), or species traits (Meiri *et al.* 2005; Novosolov & Meiri 2013).

3. Towards a macroecological synthesis of island floras

Although they account for only c. 5% of the global land surface, the world's islands harbour a disproportionately high number of native and endemic plant species (Kier *et al.* 2009). An estimated 50,000 to 70,000 vascular plants are endemic to islands (Kreft *et al.* 2008; Bramwell & Caujapé-Castells 2011), and globally, five out of 20 global centres of vascular plant diversity (Barthlott *et al.* 2005) and 20 out of 34 biodiversity hotspots (Myers *et al.* 2000), are islands, parts of islands or contain an important insular part (Kreft *et al.* 2008; Caujape-Castells *et al.* 2010). Endemic island plants include representatives of iconic island radiations (e.g. Hawaiian lobeliads and silverswords or Macaronesian Aeonium and Echium, Givnish 2010) as well as relict lineages, witnesses of early plant evolution (e.g. Amborella trichopoda on New Caledonia, Morat 1993; or the Macaronesian Apollonias barbujana, Fernández-Palacios *et al.* 2011).

Island ecosystems are under threat. Out of c. 80 recorded plant extinctions in the last 500 years, c. 50 were island species (Sax & Gaines 2008), and 39% of species facing imminent extinction are island species (not only plants; Ricketts *et al.* 2005). Between 3,500 and 6,800 endemic plant species on islands worldwide might be highly threatened, and between 2,000 and 2,800 may be in critical danger of extinction (Caujape-Castells *et al.* 2010). Islands in particular are threatened by biological invasions, habitat loss and climate change (Denslow 2003; Hassan *et al.* 2005; Sax & Gaines 2008; Kier *et al.* 2009; Caujape-Castells *et al.* 2010; Kueffer *et al.* 2010; Wetzel *et al.* 2012; Wetzel *et al.* 2013). Due to unused resources, unoccupied habitats and a lack of competitors and predators, many island communities are highly invasible (Kueffer *et al.* 2010) and thereby susceptible to invasion-caused extinctions and biotic homogenization (Shaw *et al.* 2010). Climate change is assumed to affect island ecosystems to a particularly strongly due to limited space for range shifts, sea level rise (Wetzel *et al.* 2012) and increasing storm intensities (Knutson & Tuleya 2004). Current human impact is higher on islands than on mainlands, and land-use-driven changes are assumed to further increase in the future (Kier *et al.* 2009).

To protect island ecosystems and the global diversity of island plants, it is essential to understand the mechanisms that drive the assembly of island floras. Under scenarios of globally changing climate, shrinking available habitat area and altered immigration patterns, it is necessary to know how the attributes that change, influence island diversity in the first place. Vascular plants show a wide variety of adaptations to different climatic conditions and of reproductive systems and dispersal modes (Donoghue 2008). Linking the distribution patterns of plant groups with common traits to physical island characteristics like area, isolation and

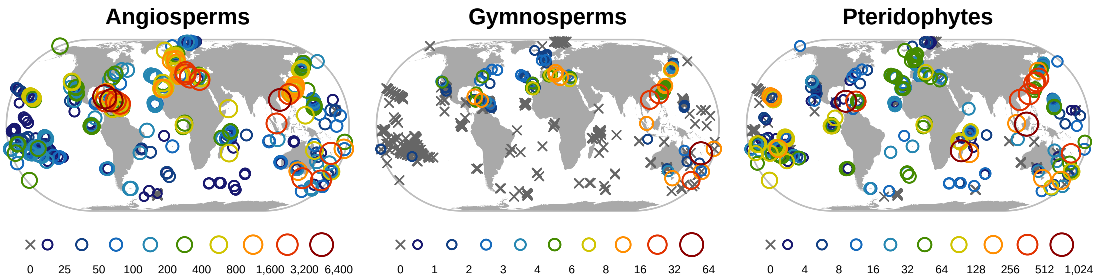

Figure I.3.1. Species numbers of native angiosperms (n = 672 islands), gymnosperms (n = 666) and pteridophytes (n = 605) on islands worldwide derived from the global database of species checklists developed for this thesis. The database comprises 1,295 checklists for 1,070 islands or island groups including 45,000 species. Only islands with comprehensive checklists for the given taxon including information on the floristic status (native vs. introduced) are shown here.

climate, helps to understand how the affected processes like immigration, establishment, speciation and extinction shape global plant diversity patterns on islands. Lessons learned from islands may further help to understand patterns and processes in mainland floras.

However, first of all it is essential to get an overview of the current state of island abiotic conditions and biotic composition. Surprisingly, no comprehensive global characterization of island environments exists so far and a macroecological synthesis is lacking. I therefore compiled datasets of both the abiotic characteristics and floristic composition of marine islands (i.e. landmasses smaller than Australia surrounded by ocean) worldwide, which serve as the data basis of my whole thesis. The abiotic database includes 85,122 high-resolution spatial island polygons derived from www.gadm.org/version1/ (Hijmans *et al.* 2009) as well as past and present bioclimatic information (Hijmans *et al.* 2005) and physical island characteristics like area, isolation, geology and elevation for 17,883 islands larger than 1 km² (see Chapter II.1). The biotic database consists of 1,295 island plant lists for 1,070 islands and island groups derived from an extensive literature survey of floras, checklists and online databases (Fig. I.3.1). The database includes c. 170,000 occurrence records of c. 45,000 native vascular plant species. Species names were processed by an automated match-up and synonymization routine using taxonomic web services (www.theplantlist.org, tnrs.iplantcollaborative.org; for details see Text V.6.1) and all unmatched genus names were checked manually. Compared to existing datasets on island plant diversity, this is, to my knowledge, the first global and most comprehensive dataset including actual species identities, allowing macroecological analyses beyond species richness.

In this thesis, I use the abiotic and biotic data to investigate how bioclimatic and physical island characteristics influence the diversity and composition of island floras at a global scale. I consider species richness, turnover among islands and phylogenetic assemblage structure as subjects of interest at varying spatial grain sizes from plot to island to archipelago level, to address the major mechanisms that shape island floras (immigration, establishment, speciation and extinction). To elucidate the role of plant characteristics related to dispersal, speciation and climatic adaptations, I perform comparative analyses among major plant groups. The comparative manner of the analyses among groups and scales and the focus on turnover and phylogenetic composition besides species richness add new perspectives to macroecological island research, allowing inferences about the mechanisms underlying global plant diversity patterns on islands. The results hence provide a step forward towards a macroecological synthesis of island floras.

4. Study outline

The research chapters of this thesis address two major aspects of the main question of what drives diversity patterns of island floras: (1) How do past and present bioclimatic and physical island characteristics (with an emphasis on the spatial arrangement of islands and archipelagos) affect plant species richness across different spatial focal units, such as vegetation plots, islands and archipelagos? (2) How do responses of species richness and phylogenetic assemblage structure to island characteristics differ among taxonomic groups with different dispersal and speciation-related characteristics, different adaptations to climatic conditions and different levels of niche and trait conservatism?

In the first research chapter (Chapter II.1), I provide a standardized bioclimatic and physical characterization of the world's islands for future use in island research and conservation. Using ordination and clustering techniques, I characterize 17,883 islands larger than 1 km² in a multidimensional environmental space and develop a standardized dataset of past and present bioclimatic variables and physical characteristics like island area, isolation, geology and elevation, to bring forward macroecological and evolutionary island research. I quantitatively compare island and mainland environments and make global predictions of insular vascular plant species richness based on statistical models.

In Chapter II.2, I address the role of differential aspects of island isolation for insular species richness. I compare ecologically meaningful metrics of isolation and quantify their relative importance in determining global vascular plant species richness on islands in a multi-predictor context based on statistical models in Kreft et al. (2008). In contrast to just measuring the distance to the nearest mainland, as commonly applied in island biogeographic studies, I consider large source islands, stepping stones, climatic similarity, wind and ocean currents and the area of surrounding landmasses as potentially important aspects of island isolation.

In Chapter II.3, I expand the perspective from single island isolation to the inter-island spatial arrangement in archipelagos. I investigate α, β, and γ diversity of vascular plants on 23 archipelagos worldwide in dependence on biogeographic predictors like area, isolation and age, bioclimatic, and intra-archipelagic spatial predictors. To this end, I develop a set of predictors describing the intra-archipelagic spatial structure of each archipelago (e.g. mean inter-island distance, connectivity and total archipelago area). To test whether main drivers of α, β, and γ diversity differ and whether γ diversity is directly affected by biogeographic, climatic and intra-archipelagic drivers or indirectly via the α and β components, I assess variable importance in linear multi-predictor models and apply structural equation models testing for the suggested indirect effects.

In Chapter II.4, I investigate whether the main physical island attributes considered by the ETIB by MacArthur and Wilson (1967), i.e. area and isolation, serve to explain species richness at the plot level. I expect that area and isolation are strong predictors of species richness only at large grain sizes and that their effects are diluted at local scales where local environmental conditions set an upper limit to species diversity and communities become saturated. Using field data on fern species richness in mountain forest plots on twelve islands in Indonesia and the Philippines, I test for the effects of area, isolation, macroclimate and local environmental conditions on species richness at varying grain sizes from plots to entire islands.

In Chapter II.5, I address the question whether major land plant groups differ in their SPARs on islands and continental settings due to group-specific differences in dispersal ability. This adds a new perspective to the thesis as I compare ecological patterns among groups with varying functional characteristics in response to island environments. I compare intercepts and slopes of SPARs for bryophytes, pteridophytes and spermatophytes on oceanic islands, continental islands, and continental areas. I expect the slope and the intercept to gradually increase from bryophytes to pteridophytes to spermatophytes. I apply a linear mixed effects modelling approach to describe variation in species richness across geological systems and taxonomic groups.

In Chapter II.6, I expand the cross-taxon comparison and investigate how dispersal and environmental filtering in combination with *in situ* speciation result in phylogenetically clustered island assemblages for angiosperms overall, palms and ferns. Dispersal- and speciation-related traits and adaptations to climate are often phylogenetically conserved within major plant lineages (Donoghue 2008). When accounting for species richness effects, phylogenetic diversity should therefore decrease with environmental factors that increase chances of dispersal to islands, be highest under environmental conditions that fit the bioclimatic requirements of more major lineages, and be negatively related to factors that increase the probability of speciation on islands. I test for differences in strength and form of these relationships for angiosperms, palms and ferns applying generalized additive models for the deviations from null expectations in phylogenetic diversity and structure of island floras in dependence on physical and bioclimatic factors, size of the source pool and biogeographic history.

Part II

Research chapters

Chapter II.1

Bioclimatic and physical characterization of the world's islands

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Abstract

The Earth's islands harbour a distinct, yet highly threatened biological and cultural diversity that has been shaped by geographic isolation and unique environments. Island systems are key natural laboratories for testing theory in ecology and evolution. However, despite their potential usefulness for research, a quantitative description of island environments and an environmental classification are still lacking. Here, we prepare a standardized dataset and perform a comprehensive global environmental characterization for 17,883 of the world's marine islands >1 km² (c. 98% of total island area). We consider area, temperature, precipitation, seasonality in temperature and precipitation, past climate change velocity, elevation, isolation, and past connectivity – key island characteristics and drivers of ecosystem processes. We find that islands are significantly cooler, wetter and less seasonal than mainlands. Constrained by their limited area, they show less elevational heterogeneity. Wet temperate climates are more prevalent on islands, whereas desert climates are comparatively rare. We use ordination and clustering to characterize islands in multidimensional environmental space and to delimit island ecoregions which provides unique insights into the environmental configuration and diversity of the world's islands. Combining ordination and classification together with global environmental data in a common framework opens up avenues for a more integrative use of islands in biogeography, macroecology, and conservation. To showcase possible applications of the presented data, we predict vascular plant species richness for all 17,883 islands based on statistically derived environment-richness relationships.

Introduction

Marine islands harbour a great part of our planet's biological and cultural diversity and provide ecosystem services to more than 500 million people (Wong *et al.* 2005). Existing estimates assign 3 to 3.6% of the Earth's land area to islands (Whittaker & Fernández-Palacios 2007; Kier *et al.* 2009) and their number exceeds 100,000, depending on threshold size (Depraetere & Dahl 2007). Islands vary greatly in geologic history, area, isolation, elevation, and climatic conditions (Wallace 1880; Whittaker & Fernández-Palacios 2007; Gillespie & Clague 2009). The complex interplay between islands' past and present environments and their isolated nature has produced biotas that differ greatly among islands and between islands and mainlands (Stuart *et al.* 2012). Islands are characterized by a high proportion of endemic species (Kier *et al.* 2009) and their unique biota are particularly susceptible to anthropogenic threats (Wong *et al.* 2005; Kueffer *et* *al.* 2010; Wetzel *et al.* 2013). Island research and conservation could make great progress with truly global analyses, but standardized data on key island biogeographic characteristics are currently lacking.

Biogeographic and macroecological research, and conservation planning, rely on spatially explicit data on both biodiversity and abiotic conditions (Ferrier 2002). For instance, knowledge on environmental and compositional representativeness and irreplaceability is necessary for conservation prioritization (Olson & Dinerstein 2002; Brooks *et al.* 2006) and requires standardized data for all locations worldwide. Global data on climatic and other environmental drivers of ecosystem processes, and ecosystem responses like productivity and vegetation structure, are becoming increasingly available at increasing resolution (Jetz *et al.* 2012a), and knowledge on the biotic constituents of ecosystems has improved greatly (Graham *et al.* 2004; Jetz *et al.* 2012a). The advent of such large environmental and biodiversity datasets has opened up opportunities for global-scale analyses and, especially for mainlands, has facilitated significant progress in research over the past decade.

Though initially restricted to model archipelagos, such as Galapagos, Hawaii, and the Canaries, island research has inspired some of the most influential theories in ecology and evolution (Darwin 1859; Wallace 1880; MacArthur & Wilson 1967; Losos & Ricklefs 2009). Recently, quantitative global analyses have also appeared (Kalmar & Currie 2006; Kreft *et al.* 2008; Kueffer *et al.* 2010), but have been restricted to a non-random subset of islands with available data. A synthesis of the macroecology of the world’s islands is still missing. While the large number, small size and discrete boundaries of islands provide exciting research opportunities (Losos & Ricklefs 2009), the same qualities have hampered the compilation of standardized data. The United Nations Environment Programme Island Directory (Dahl 2004) was a first step towards a global overview, providing information on c. 2,000 islands. More recently, scientific knowledge on physical and biological aspects of select islands and archipelagos was summarized (Gillespie & Clague 2009) and the "Global Island Database" made available information for conservation and policy making (gid.unep-wcmc.org). Despite such first steps towards a global island dataset, a rigorous, standardized, and quantitative characterization of the world's islands is still lacking.

From a biological perspective, islands are inherently different from continental areas and drivers of these differences are key to understanding processes and patterns on islands (Wong *et al.* 2005). In island biogeographic theory, isolation and area are considered the most important drivers of island biodiversity (MacArthur & Wilson 1967; Whittaker & Fernández-Palacios 2007). Speciation predominantly occurs on large and isolated islands and large islands are more likely to maintain viable populations of many species (Heaney 2000; Losos & Schluter 2000; Kisel & Barraclough 2010; Rabosky & Glor 2010). Isolation affects island biota in complex

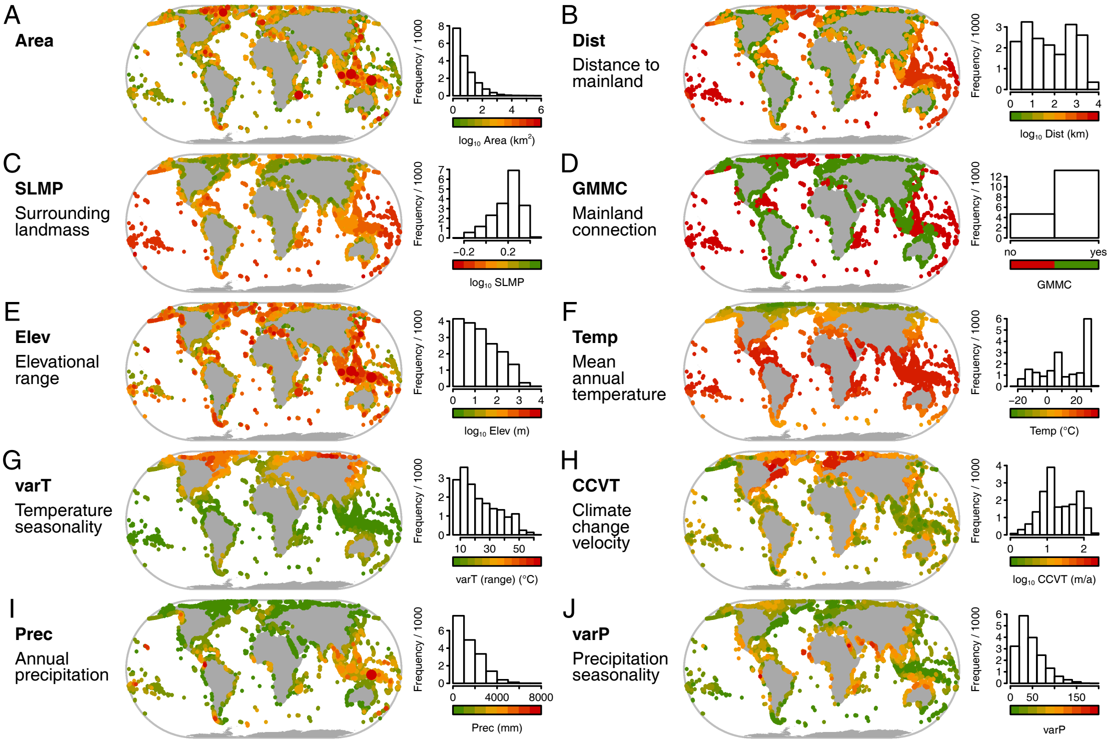

Figure II.1.1. Global patterns of key physical and bioclimatic variables on 17,883 marine islands >1 km². (A) Island area (*Area*), (B) distance to mainland (*Dist*), (C) surrounding landmass proportion (*SLMP*), (D) glacial maximum mainland connection (*GMMC*), (E) elevational range (*Elev*), (F) annual mean temperature (*Temp*), (G) temperature seasonality (*varT*), (H) climate change velocity in temperature (*CCVT*), (I) annual precipitation (*Prec*), (J) precipitation seasonality (*varP*). Points are plotted in order of decreasing frequency, i.e. islands with rare environments are plotted on top of islands with common characteristics if points overlap.

ways (22). For instance, the amount of surrounding landmass may determine the number of arriving propagules and the over-water distance may act as a dispersal filter causing compositional disharmony - an underrepresentation of certain taxonomic or ecological groups (Carlquist 1965). However, a comprehensive framework for global island research requires going beyond classical island biogeographic determinants (Triantis *et al.* 2008). Age and time-area dynamics are key predictors of the diversity of evolutionary arenas (Jetz & Fine 2012) and consequently island age and geology (e.g. volcanic vs. continental) represent core factors for understanding island biodiversity (Heaney 2000; Whittaker *et al.* 2008). In addition, macroclimate, heterogeneity, and climate stability are known to influence endemism, assembly and phylogenetic structure of island communities (Kreft *et al.* 2008; Hortal *et al.* 2009; Sandel *et al.* 2011; Kissling *et al.* 2012b).

Areas within which ecosystems share certain characteristics may be defined as "ecoregions" (Bailey 1998). Delineations may be based on biotic composition, evolutionary legacy, drivers of ecosystem processes (e.g. temperature), or measures of ecosystem responses (e.g. productivity; Mackey *et al.* 2008). Biomes, e.g., describe regions of similar vegetation structure determined by temperature and precipitation (Holdridge 1947; Whittaker 1975; Kottek *et al.* 2006). Often, criteria for delineations are not well defined. For instance, the widely used World

Wildlife Fund ecoregion classification represents an expert-based assessment of both the distinctiveness of biotic assemblages and proxies such as vegetation structure (Olson *et al.* 2001). More quantitative classifications, made possible by the increasing availability of information, efficient algorithms and computational power have appeared recently (Hargrove & Hoffman 2004; Mackey *et al.* 2008; Kreft & Jetz 2010; Metzger *et al.* 2013), but islands are often underrepresented or altogether excluded, due to their small size.

Here, we aim to provide a comprehensive environmental synopsis and classification of the world's islands. We (I) provide a comprehensive multivariate characterization and a standardized dataset of island bioclimatic and physical conditions; (II) compare island and mainland environments; (III) explore multivariate approaches for delineating environmental island ecoregions; (IV) provide general perspectives how this unique multivariate characterization may be used in island research and management and (V) implement an example application by making environment-based predictions of vascular plant species richness on islands worldwide.

Results and Discussion

Island environments

Our bioclimatic and physical characterization of the world's islands considered 85,122 marine islands smaller than Greenland. These islands comprise c. 7.84 x 10^6 km², or 5.3% of the Earth's land area, significantly exceeding previous estimates of 3 to 3.6% (Whittaker & Fernández-Palacios 2007; Kier *et al.* 2009). 65,730 islands in the dataset are smaller than 1 km², but they make up only 0.17% of overall island area. Hence, island sizes show a strongly right-skewed distribution (17 islands >100,000 km²; Fig. V.1.1). How many islands exist in total cannot be straightforwardly estimated. Fractal theory predicts island number to increase with decreasing minimum considered island area, up to millions of smallest islets and rocks (Depraetere & Dahl 2007). We focused on islands >1 km², which is biologically justifiable because on small islands speciation events and endemism are rare (Losos & Schluter 2000; Kisel & Barraclough 2010) and stochastic forces drive diversity patterns (Lomolino & Weiser 2001). Out of 19,392 islands >1 km², 17,883 had sufficient environmental information for a detailed assessment of bioclimatic and physical conditions (Fig. II.1.1, Table V.1.1). Together they comprise c. 7.67 x 10^6 km², i.e. 5.2% of the Earth's land area and 97.8% of total island area, and serve as a solid baseline for an abiotic characterization of the world's islands.

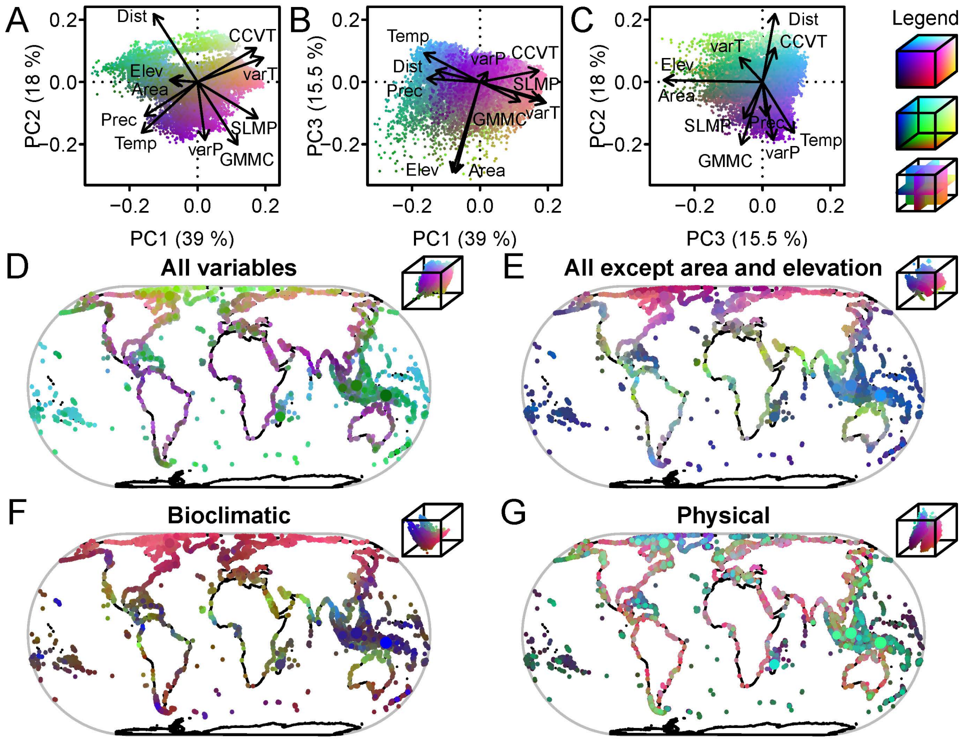

Figure II.1.2. Principal component analyses (PCA) based on bioclimatic and physical variables for 17,883 marine islands >1 km² worldwide. (A-C) Biplots of the first three PCA axes when all ten variables are included. (D-G) Maps of ordination site scores: (D) all ten variables, (E) all variables but *Area* and *Elev*, (F) contemporary bioclimatic variables only (*Temp*, *varT*, *Prec*, *varP*), and (G) physical variables only (*Area*, *Dist*, *SLMP*, *GMMC*, *Elev*). Colors refer to a red-green-blue (RGB) color space (cubes in legend) projected onto the respective three-dimensional PCA-space. Hence, in A-D each island consistently has the same color. Cubes in D-G show PCA results in a three dimensional space. In A-C points are plotted in decreasing order of the respective component not shown to give an impression of three-dimensionality, in D-G in decreasing order of island area, plotting the rare large islands on top if points overlap. Abbreviations follow Fig. II.1.1.

Contrary to what some map projections suggest, Hawaii is not the most remote archipelago. The most remote islands belong to the Society and Austral Islands and Western Tuamotu (French Polynesia; Fig. II.1.1B). Tahiti, c. 5,900 km from the nearest mainland, is the largest of these islands. In terms of surrounding landmass (Weigelt & Kreft 2013), the most isolated islands lie east of Australia (from Macquarie Island to Fiji; Fig. II.1.1C), including New Zealand and New Caledonia, islands of outstandingly high endemism richness (Kier *et al.* 2009). Assuming a decrease in sea levels of 122 m (Miller *et al.* 2005), about 75% of all islands were probably connected to a continent during the last glacial maximum (LGM; Fig. II.1.1D). Such land bridges could have allowed biotic exchange between and homogenization of the respective island and mainland assemblages. Isolated evolution on unconnected islands, in contrast, may have preserved unique assemblages, including relict endemics on old continental fragments and iconic adaptive radiations on volcanic archipelagos (Cronk 1997; Losos & Ricklefs 2009).

65% of all islands are non-tropical. Annual mean temperature and temperature seasonality follow typical latitudinal trends (Fig. II.1.1F-G). Past climate change velocity, i.e. the speed needed to track the mean annual change in temperature since the LGM (21,000 a BP), while accounting for variation in topographic complexity, is highest on North Atlantic islands (Fig. II.1.1H), which is consistent with Sandel *et al.* (2011). Precipitation is highest on tropical and highly elevated islands (Fig. II.1.1I), with high intra-archipelago variation. For instance, within the Marquesas, only islands higher than 800 m receive rainfall exceeding 3,000 mm/a. Consequently, they harbour cloud and rain forests and differ from lower islands in composition and richness (Florence & Lorence 1997). In contrast, flat islands can be extremely dry. Precipitation seasonality is highest on tropical islands at western continental coasts (e.g. Isla Lobos de Tierra, Peru, and Cape Verde).

Some island characteristics are strongly correlated (Fig. V.1.2, Table V.1.2). We found highest correlations between isolation metrics and mainland connection, among climatic variables, and between area and elevation. Some of these correlations are underlain by simple geometric constraints. For instance, high mountains require a minimum area and remote islands are unlikely to have had past mainland connections. For a subset of 102 volcanic islands for which we obtained estimates of geologic age since emergence, island age was not related to area (as raw variable, $P = 0.62$; $\log_{10}$-transformed, $P = 0.96$; as quadratic term, $P = 0.77$). In theory, the area of a volcanic island increases after its emergence and decreases after volcanic activity has stopped (Whittaker *et al.* 2008), but the expected hump-shaped relationship between age and area may only be noticeable within geologically homogeneous systems like single archipelagos. However, we found a significant negative correlation between island age and elevational range ($r = -0.25$, $P < 0.05$), possibly reflecting the effect of erosion on island height.

We performed principal component analysis (PCA) to reduce correlated variables to independent components and visualize island characteristics in fewer dimensions (Fig. II.1.2A-C, Fig. V.1.3). The first three axes of a PCA including all ten bioclimatic and physical variables accounted for 72.4% of the variance, with the most important axis (39%) representing primarily bioclimatic variables (Fig. II.1.2A-B, Table V.1.3). Isolation and mainland connection metrics varied mainly along the second axis, almost separating the islands into two groups (Fig. II.1.2A). The third axis separated small, flat islands from large, high islands, with most islands falling on the small, flat end (Fig. II.1.2B). Visualized on a world map (Fig. II.1.2D), the PCA results allow identification of groups of islands with similar characteristics. An abrupt change occurred at the transition from continental to oceanic islands. Within these groups, we detected more gradual changes along physical and bioclimatic axes. These gradients were even more pronounced when PCA was applied to current bioclimatic (Fig. II.1.2F) or physical variables separately (Fig. II.1.2G).

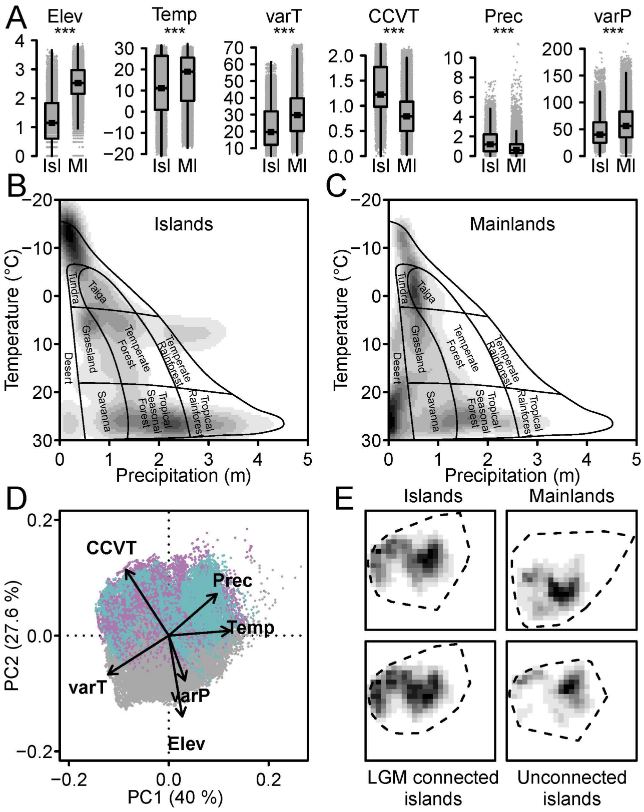

Figure II.1.3. Island vs. mainland comparisons. (A) Elevational range (*Elev*; $\log_{10}$ m), annual mean temperature (*Temp*, °C), annual temperature range (*varT*, °C), past climate change velocity in temperature (*CCVT*, $\log_{10}$ (m/y)), annual precipitation (*Prec*, m), and variation in precipitation (*varP*) compared for 17,883 islands >1 km² (Isl) and 42,985 equal area mainland grid cells (Ml). Significance of differences was assessed using Mann-Whitney-U-tests (*** $P < 0.001$). Boxes represent the interquartile range around the median; whiskers extend 1.5 times the interquartile range from the box. (B) Densities of islands and (C) mainland grid cells plotted onto Whittaker's scheme of biomes (Whittaker 1975) delineated on the basis of *Temp* and *Prec*. (D) PCA for 4,676 oceanic islands (cyan), 13,207 continental islands (magenta) and mainland grid cells (grey). (E) Kernel densities of geologic subsets along the first two PCA axes.

Island – mainland comparison

Island and mainland characteristics differed markedly. Elevational range was significantly lower on islands than in mainland grid cells (Fig. II.1.3A). While this is partly due to the small size of most islands compared to the coarse mainland grain, limited area is also an intrinsic island feature that precludes elevational ranges comparable to mainland mountain regions. Significantly lower seasonality and higher precipitation on islands indicate lower climatic continentality than on mainlands (Fig. II.1.3A). Due to a large number of Arctic islands, annual mean temperatures were lower on islands, whereas past climate change velocity was significantly higher, with especially high values in the Canadian Arctic Archipelago. In a common PCA space, islands and mainland regions occupied different areas (Fig. II.1.3D-E). The first two axes explained 68.6% of the variation and uncovered the most striking differences, as kernel densities were uncorrelated among islands and mainlands ($r = 0.07$, $P > 0.05$). For other axis combinations, kernel density correlations were significant (PC1/PC3: $r = 0.72$, PC2/PC3: $r = 0.16$, both $P < 0.001$). Kernel densities of islands connected to the mainland during the LGM and unconnected islands were significantly correlated, indicating that they occupy a similar environmental space (PC1 and PC2: $r = 0.75$, PC1 and PC3: $r = 0.65$, PC2 and PC3: $r = 0.88$, all $P < 0.001$). We projected islands onto the classic Whittaker plot of biomes (Whittaker 1975) classified by annual mean temperature and precipitation (Fig. II.1.3B-C). Overall, cold climates and wet climates were over-represented on islands, and warm and dry

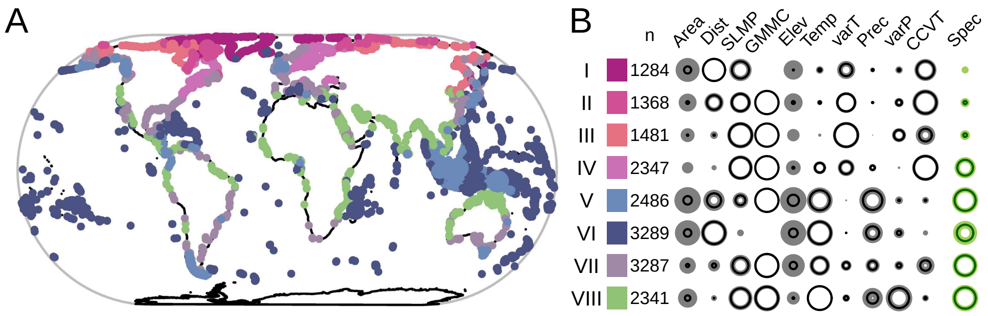

Figure II.1.4. PAM clustering of weighted PCA axes for 17,883 islands >1 km² based on eight environmental variables (all except *Area* and *Elev*). Colors in the map (A) were calculated as mean RGB values of all islands per cluster based on the PCA in Fig. II.1.2E. Points were plotted in decreasing order of *Area*. Circles in B indicate variable characteristics within the clusters: Circle = arithmetic mean; shaded ring = standard deviation. Abbreviations follow Fig. II.1.1. *Spec* indicates predicted vascular plant species richness.

climates under-represented. Tropical and especially temperate rainforests were over-represented on islands, which is notable because temperate rainforests are among the rarest ecosystems on Earth (Olson & Dinerstein 2002).

Quantitative island regionalizations

We produced a set of classifications of global islands to provide a first environment-driven island ecoregion framework. Because area and elevational range showed no or only low spatial autocorrelation (Table V.1.1), a regionalization considering these variables generated disjunct ecoregions, reflecting that small, flat islands may occur next to large, high islands (Fig. V.1.4). Including only bioclimatic and physical variables with a high level of spatial autocorrelation (Moran's I values from 0.59 to 0.99, all $P < 0.001$) generated more contiguous ecoregions (Hargrove & Hoffman 2004). Excluding area and elevational range and using non-hierarchical clustering (partitioning around medoids, PAM) of weighted PCA axes, we identified eight distinct sets of islands (Figs. II.1.4 & V.1.5, Table V.1.4): Clusters I-IV included northern temperate to Arctic islands, with II-IV characterized by LGM mainland connections and differentiated by bioclimate. Clusters V-VIII consisted of temperate to tropical islands, with VI including the majority of highly isolated oceanic islands. The lack of further divisions among highly isolated oceanic islands highlights their comparatively homogeneous bioclimatic conditions. Although this ecoregionalization offers a first quantitative baseline for the world's island environments, the specific outcome is contingent on the number of groups chosen and the clustering algorithm. Using the unweighted pair-group method with arithmetic mean (UPGMA) instead of PAM produced groups of vastly different sizes (1 - 7,092 islands per cluster compared to 1,284 - 3,289 islands per cluster; Fig. V.1.6), highlighting the methodological sensitivity of the clustering approach. The application of environment-based

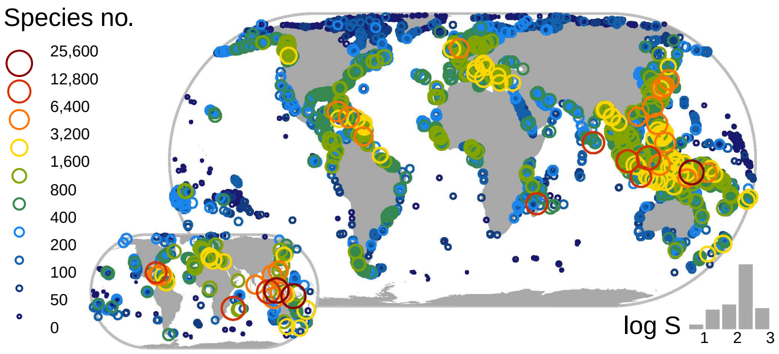

Figure II.1.5. Predictions of vascular plant species richness for 17,883 islands >1 km² (constituting c. 98% of global island land area) worldwide based on generalized additive models and model averaging. Predictors include the ten bioclimatic and physical variables presented here, richness of the nearest mainland region and spatial position on the sphere. Circles were plotted in order of increasing species richness. The embedded map indicates the observed species richness of vascular plants for 475 islands used to train the model. The histogram shows the frequency distribution of $\log_{10}$ species richness.

regionalizations is also limited by the gradual nature of most environmental changes, which compromises the idea of strict distinctions. Multivariate measures of environmental similarity based on PCA analyses and as mapped in Fig. II.1.2 may represent a more appropriate and powerful tool to account for gradual changes when analyzing and visualizing regional affinities. We suggest carefully checking the results of both the ordination and clustering steps.

Richness predictions

To showcase possible applications of the presented data and multivariate framework, we used it to predict the species richness of native vascular plants on all 17,883 islands >1 km². Specifically, we used a multi-model approach (Burnham & Anderson 2002) and included as predictors the ten presented bioclimatic and physical variables, richness of the nearest mainland region, and spatial position on the sphere (Fig. II.1.5, Table V.1.5). The averaged model achieved remarkably strong fits with observed richness on the 475 islands used for training (Fig. V.1.7; pseudo R2 = 0.936, averaged mean error based on 10-fold cross validation = 0.031; not accounting for spatial non-independence). The Southeast Asian Archipelago, the Caribbean and the Mediterranean emerged as richness centres, attributable to their many large islands, (sub)tropical climates, low degrees of isolation and high regional mainland diversity (Fig. II.1.5). Oceanic islands were on average less diverse than continental islands with only few exceptionally diverse islands (Figs. II.1.4 & II.1.5). The generalized additive modelling approach presents a flexible way to account for multiple non-linear effects and complex interactions, as well as spatial richness variation (Wood 2003). However, the model underestimated species richness on some large, tropical islands (compare Fig. V.1.7) and overestimated it on others (e.g. Britain). While the model captures the interplay of bioclimatic and physical drivers of insular plant species richness, the predictions only account for the variables selected and do not mechanistically address the historical biogeography of the different plant clades found on islands. We therefore caution against their use without contemplation. Nevertheless, the predictions give a first global overview of vascular plant species richness on islands and may provide a good baseline prediction against which to test ecological and evolutionary processes in island biogeography.

Perspectives

In contrast to alternative global frameworks (Metzger *et al.* 2013), our study specifically focuses on islands. It represents a first step towards a thorough characterization of the world's islands for island research and conservation. The data may help to address questions in ecology and evolution, such as whether the unique diversity of islands and speciation patterns are due to isolation and lack of gene flow or if island evolution differs from mainland evolution due to environmental differences (Barton 1998). The framework also has great potential for island conservation. Island biota are particularly threatened, by biological invasions, habitat loss and changing climate (Wong *et al.* 2005; Kier *et al.* 2009; Kueffer *et al.* 2010; Wetzel *et al.* 2013). The majority of historically recorded vertebrate extinctions occurred on islands and 39% of species facing imminent extinction are island species (Ricketts *et al.* 2005). Island communities are highly susceptible to invasion-induced extinction and biotic homogenization (Kueffer *et al.* 2010; Shaw *et al.* 2010). Assessing environmental similarity may help to connect potential source and target areas for invaders and aid in proactive measures. Further, climate change particularly affects island ecosystems due to sea level rise and limited space for range shifts (Wong *et al.* 2005; IPCC 2007; Wetzel *et al.* 2013). We identified islands of high past climate change velocity and areas where species may track future changes in a heterogeneous topography. Finally, human impact is higher on islands and land-use-driven changes will still increase (Kier *et al.* 2009). An ecoregion framework may assist in assessing habitat loss and conversion and identifying areas of high representativeness, distinctiveness and priority for nature conservation (Olson & Dinerstein 2002; Brooks *et al.* 2006).

Our approach is limited by the accuracy of the underlying bioclimatic and physical data (Text V.1.1), and because it is purely environment-based. However, the richness models indicate that the environmental factors strongly relate to biogeographic factors. Once available at the global scale, biotic similarity could be used in combination with an abiotic characterization to quantitatively delimit island biogeographic regions that account directly for biogeographic history (Olson *et al.* 2001; Kreft & Jetz 2010). Until then, the data and approaches described here can serve as a baseline and source for developing and testing hypotheses, and for identifying islands of particular environmental uniqueness or representativeness and the predictions of vascular plant species richness can aid in identifying islands of outstanding biodiversity. The standardized dataset (Weigelt *et al.* 2013b) (download at dx.doi.org/10.5061/dryad.fv94v) and quantitative nature of our characterization and ecoregionalization may contribute to more rigorous and reproducible approaches in island research and conservation.

Materials and Methods

Islands

We defined islands as landmasses surrounded by ocean and smaller than Greenland. This excludes freshwater islands. As geographic reference, we used the GADM database,version 1 (Hijmans *et al.* 2009), which includes 85,122 high-resolution island polygons. We focused on all 19,392 islands >1km². Comparison with 90 m resolution elevation data (srtm.csi.cgiar.org) confirmed that these polygons include most islands >1km² worldwide. For 17,883 islands, we could assemble complete environmental information. The 1,509 missing islands were distributed evenly across island-rich regions of the globe and were only slightly larger than 1 km² (Fig. V.1.1).

Physical variables

We considered five bioclimatic and five physical variables describing the exogenous physical environments of islands (Mackey *et al.* 2008). Island area (*Area*) was calculated for each GADM polygon in cylindrical equal area projection. Although polygon area differs from actual surface area, which is influenced by island topography, it is an adequate approximation (Triantis *et al.* 2008). As measures of isolation, we used the distance to the nearest mainland (*Dist*) and the proportion of surrounding landmass (*SLMP*). *Dist* was calculated as the shortest great circular distance between an island's mass centroid and the mainland coast. This metric is as good an isolation metric at a global scale as the distance from the island coast (Weigelt & Kreft 2013), but its calculation is computationally less demanding. Antarctica was not considered as mainland due to its permanent ice cover. We calculated *SLMP* as the sum of the proportions of landmass within buffer distances of 100, 1,000 and 10,000 km around the island perimeter. *SLMP* has been shown to be the best isolation metric to island plant diversity at a global scale (Weigelt & Kreft 2013). Unlike other isolation metrics, *SLMP* accounts for coastline shape of large landmasses by considering only regions that extend into the measured buffers. As a coarse proxy for island geological history, we noted whether an island was connected to the mainland during the LGM (*GMMC*), assuming a sea level at 18,000 a BP of 122 m below the present level (Miller *et al.* 2005). More sophisticated geologic data are not available at reasonable spatial resolution, but *GMMC* differentiates well between oceanic and continental islands (Fig. II.1.1D). We included the maximum elevation of each island as a measure of topographic complexity and a proxy for environmental heterogeneity (*Elev*). *Elev* relates to the number of available habitats as a result of differences between wind- and leeward sites, temperature decrease with altitude, and high precipitation regimes in certain altitudinal belts (Allouche *et al.* 2012). Elevation data at 30 sec. resolution was from Hijmans *et al.* (2005). For 1,891 small islands that did not fully enclose a 30 sec. raster cell, we applied a 1 km buffer to the island perimeter.

Bioclimatic variables

For most islands, bioclimatic variables came from WorldClim (Hijmans *et al.* 2005). We used maximum values of annual mean temperature (*Temp*) and annual precipitation (*Prec*), as these are key drivers of ecosystem processes, vegetation structure (Bailey 1998), and species richness (Kreft *et al.* 2008). Intra-annual seasonality was quantified using the minimum annual temperature range (*varT*) and the minimum coefficient of variation in monthly precipitation (*varP*). We focused on extreme values rather than spatial means to capture the climatically most favourable part of each island. A region of French Polynesia and the Pitcairn islands including 129 islands >1 km^2, including important volcanic islands like the Marquesas, was not covered by WorldClim temperature data. We therefore modelled *Temp* and *varT* for these islands based on the strong correlation of sea surface and air temperatures of neighbouring islands (Text V.1.1). We calculated climate change velocity in temperature (*CCVT*) since the LGM 21,000 a BP as the ratio between temporal change and contemporary spatial change in temperature at 30 sec. resolution (Sandel *et al.* 2011) and extracted mean values for each island (Text V.1.1). Because of the higher uncertainty in paleoclimatic reconstructions of precipitation (Sandel *et al.* 2011), we did not include climate change velocity in precipitation. We acknowledge the limitations of the bioclimate datasets, as the WorldClim model interpolates from weather station observations using latitude, longitude and elevation (Hijmans *et al.* 2005). Climate predictions in regions with poor station density and varied topography have limited reliability (Soria-Auza *et al.* 2010).

Island age

For 102 volcanic islands unconnected to the mainland during the LGM, we assembled island ages, an important determinant of species diversity and endemism (Whittaker *et al*. 2008), from primary research literature and compilations (e.g. Gillespie & Clague 2009). Due to the small sample size, island age did not enter multivariate analyses but we assessed its relation to other variables.

Statistical analyses

Area, *Elev* + 1, *Dist* + 1, *SLMP* + 0.5 and *CCVT* + 1 were $\log_{10}$-transformed to reduce skewness and to moderate extreme values. Small constants were added to avoid taking the logarithm of zero. We assessed spatial autocorrelation using Moran's I values. Collinearity was evaluated using pairwise correlations. Coefficients and significances were corrected for spatial autocorrelation following Dutilleul *et al.* (1993). We performed PCAs of both including all standardized variables and for the following subsets: all variables but *Area* and *Elev,* contemporary bioclimatic variables only (*Temp*, *varT*, *Prec*, *varP*), and physical features only (*Area*, *Dist*, *SLMP*, *GMMC*, *Elev*).

To compare the environmental characteristics of islands and mainlands, we performed a PCA of all 17,883 islands and 42,985 equal area mainland grid cells spanning all continental areas worldwide (each 3,091 km² but covering less landmass in coastal areas). As input variables, we used all bioclimatic and physical variables not restricted to islands (*Elev*, *Temp*, *varT*, *Prec*, *varP* and *CCVT*). We used kernel densities in PCA biplots as a measure of occupancy and correlated them among geologic units (all islands, islands connected to mainland at the LGM, unconnected islands, mainlands).

To delimit island regions of similar bioclimatic and physical conditions, we performed cluster analyses based on the ten environmental variables and the variable subsets mentioned above. We used agglomerative hierarchical (UPGMA) and non-hierarchical clustering methods (PAM). UPGMA produces a cluster dendrogram representing the relatedness of the delimited regions. From the dendrogram, a preferred number of clusters can be inferred (Milligan & Cooper 1985). PAM requires a specified number of clusters in advance and does not provide relationships among regions. However, PAM tends to delineate clusters of similar size and upper limits of within-group variance, preventing the creation of regions that greatly differ in within-region variance (Hargrove & Hoffman 2004). Due to the strong collinearity of some variables, we used Euclidean distances on PCA axes as input distances; these are most appropriate because of the orthogonal nature of the PCA space (Kaufman 1985). PCA axes were weighted by the square root of their eigenvalues to reduce the influence of less important axes (Kaufman 1985). We chose a number of clusters small enough for presentation and discussion based on the Caliński and Harabasz index (Milligan & Cooper 1985).

Environment-richness model and global prediction

As example application of the integrated physical and bioclimatic island data we produced species richness predictions for all 17,883 islands >1 km². The modelling approach builds on previous work (Kreft *et al.* 2008; Weigelt & Kreft 2013). For 475 islands we collected numbers of native vascular plant species per island from floras, checklists and compilations (Kreft *et al.* 2008; Weigelt & Kreft 2013) (Text V.1.1). As predictor variables, we used the presented physical and bioclimatic variables, and vascular plant richness in the nearest mainland grid-cell of the co-kriging data in Kreft and Jetz (2007) to reflect historical biogeographic influences on the available species pool. We used generalized additive models including penalized regression splines with up to three degrees of freedom, and an isotropic smooth of latitude and longitude on a sphere to account for spatial patterns in the response variable (Wood 2003). We allowed tensor product interactions among *Area* and *Temp*, *Dist* and *SRML*, *Temp* and *Prec*, and *Area* and *Dist*. We made predictions based on multiple candidate models weighted by model fit (Burnham & Anderson 2002) and used 10-fold cross validation to estimate prediction errors. Methods and results of alternative modelling approaches can be found in Text V.1.1, Fig. V.1.7 and Table V.1.5.

All bioclimatic and physical variables, ordination and clustering results, richness values of the nearest mainland grid cell and predicted vascular plant species richness values per island are available at the dryad data repository (dx.doi.org/10.5061/dryad.fv94v) (Weigelt *et al.* 2013b).

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Chapter II.2

Quantifying island isolation – insights from global patterns of insular plant species richness

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Abstract

Isolation is a driving factor of species richness and other island community attributes. Most empirical studies have investigated the effect of isolation measured as distance to the nearest continent. Here we expanded this perspective by comparing the explanatory power of seventeen isolation metrics in sixty-eight variations for vascular plant species richness on 453 islands worldwide. Our objectives were to identify ecologically meaningful metrics and to quantify their relative importance for species richness in a globally representative dataset. We considered the distances to the nearest mainland and to other islands, stepping stone distances, the area of surrounding landmasses, prevailing wind and ocean currents and climatic similarity between source and target areas. These factors are closely linked to colonization and maintenance of plant species richness on islands. We tested the metrics in spatial multi-predictor models accounting for area, climate, topography and island geology. Besides area, isolation was the second most important factor determining species richness on the studied islands. A model including the proportion of surrounding land area as the isolation metric had the highest predictive power, explaining 86.1% of the variation. Distances to large islands, stepping stone distances and distances to climatically similar landmasses performed slightly better than distance to the nearest mainland. The effect of isolation was weaker for large islands suggesting that speciation counteracts the negative effect of isolation on immigration on large islands. Continental islands were less affected by isolation than oceanic islands. Our results suggest that a variety of immigration mechanisms influence plant species richness on islands and we show that this can be detected at macro-scales. Although the distance to the nearest mainland is an adequate and easy-to-calculate measure of isolation, accounting for stepping stones, large islands as source landmasses, climatic similarity and the area of surrounding landmasses increases the explanatory power of isolation for species richness.

Introduction

The discrete, isolated nature of islands makes them useful units for evolutionary and ecological studies (Whittaker & Fernández-Palacios 2007), and has enabled island biogeography to contribute considerably to the development of theory on the origin and the maintenance of species richness (Lomolino & Brown 2009). According to the equilibrium theory of island biogeography, species richness on islands results from a dynamic equilibrium between the opposing processes of immigration and extinction (MacArthur & Wilson 1967). Assuming immigration to happen more frequently on less isolated islands, MacArthur and Wilson considered isolation as one of the main factors influencing species richness. Although these authors considered the importance of evolutionary processes, they excluded phylogenetic diversification from the equilibrium theory, arguing that speciation becomes important only on the largest and most isolated islands. More recent models have emphasized the role of evolutionary processes at large time scales for the assembly and species richness of biotas on oceanic islands. According to Whittaker *et al.* (2008), oceanic islands show varying rates of immigration, speciation and extinction over time when emerging from volcanic activity or submerging from erosion. In fact, speciation may act on the same time scale and be of similar quantitative importance for species richness as immigration and extinction (Heaney 2000; Carroll *et al.* 2007) as evidenced by the high degree of insular endemism (Kier *et al.* 2009).

The principal effect of isolation on species richness results from an inverse relationship with the probability of dispersal to an island, influencing the chance of colonization (MacArthur & Wilson 1967). Particularly on small and less isolated islands, the continuous arrival of propagules might in addition increase population viabilities of species present on the island via a 'rescue effect' (Brown & Kodric-Brown 1977). Consequently, overall species richness should be negatively correlated to island isolation. However, the effect of isolation on large islands is decreased by a 'target area effect', i.e. large islands receive more immigrants (Whitehead & Jones 1969). Furthermore, gene flow between source and island populations should be negatively correlated to isolation, leading to a higher probability of speciation on remote islands (Heaney 2000). Especially on large and heterogeneous islands, cladogenesis (in situ speciation; Stuessy *et al.* 2006) thus counteracts the negative effect of isolation on immigration (Heaney 2000; Losos & Schluter 2000; Kisel & Barraclough 2010).

Many empirical studies have investigated the effect of isolation on species richness for various taxa and from local to global scales. Most studies have found strong support for the expected negative relationship (e.g. Johnson & Simberloff 1974; Kalmar & Currie 2006; Kreft *et al.* 2008). Others have found little or no significant effect of isolation (e.g. Abbott 1978; Price 2004; Cody 2006), particularly when study systems were of limited spatial extent and exhibited little variation in isolation (for a review see Whittaker *et al.* 2001).

While conceptual models in island biogeography commonly consider isolation as the 'distance to', or more generally as 'isolation from' an unspecified source pool, correlative studies require a precise metric quantifying isolation. Many different metrics have been tested. The vast majority of studies have used the distance between a target island and the nearest mainland coast (e.g. Case 1975; Abbott 1978; Chown *et al.* 1998) since continental landmasses harbour large species pools for potential island colonization. The validity of this approach is supported by

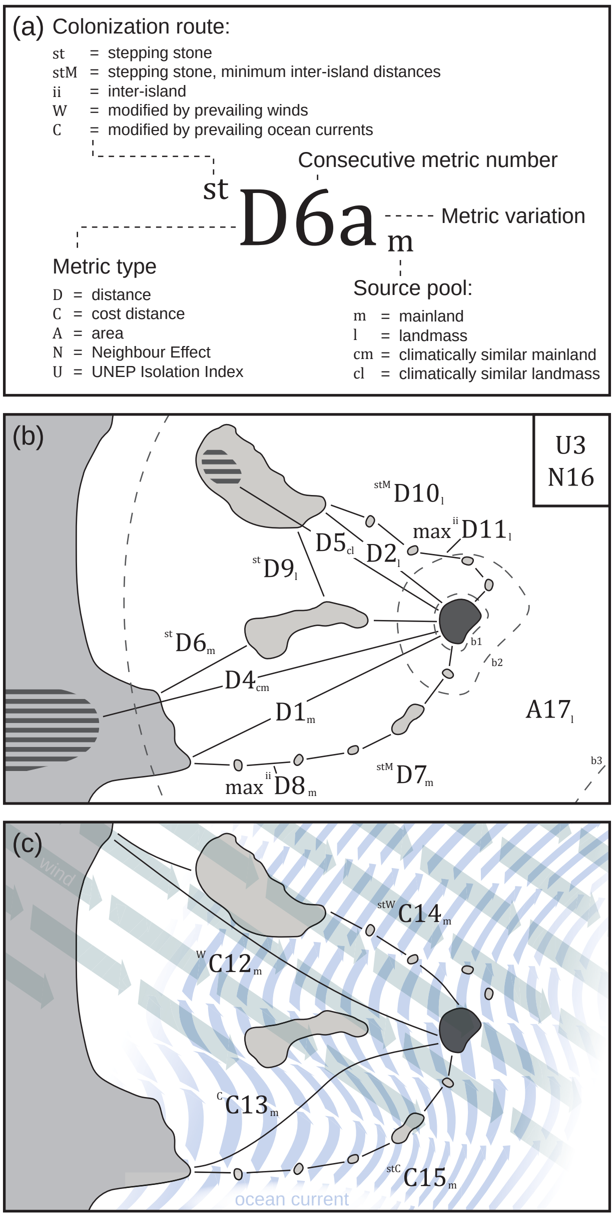

Figure II.2.1. (a) Symbology for isolation metrics used in this study. (b-c) Schematic representation of hypothesized island immigration pathways of seventeen tested isolation metrics. These metrics reflect (b) measures of geographic distance, stepping stone distance, and surrounding landmass area as well as (c) the influence of prevailing winds (straight grey arrows) and ocean currents (curved blue arrows). In both (b) and (c), the target island is coloured dark grey; the mainland is located on the left. max^{ii}D8$_m$ and max^{ii}D11$_l$ refer to the longest inter-island distance along a stepping stone path, whereas stD6$_m$, ^{stM}D7$_m$, stD9$_l$, ^{stM}D10$_l$, ^{stW}C14$_m$ and ^{stC}C15$_m$ refer to the full path between source landmass and target island. In (b), hatched regions indicate areas climatically similar to the target island. b$_1$ to b$_3$ indicate buffer zones around the target island for calculation of surrounding landmass proportions (A17$_l$). Metrics U3 and N16 are not shown graphically.

phylogenetic studies indicating long-distance dispersal events from continents to even remote islands (e.g. Alsos *et al.* 2007; Harbaugh & Baldwin 2007). However, islands may also serve as sources for immigration to other islands and to the mainland (Bellemain & Ricklefs 2008; Keppel *et al.* 2009). The distance to the nearest island (Johnson & Simberloff 1974), the nearest large or larger island (McMaster 2005), the nearest older island (Cardoso *et al.* 2010), or the mean distance to other islands (Borges & Hortal 2009) have therefore been used in correlative studies. The UNEP Isolation Index (Dahl 2004), another frequently used metric (e.g. in Boyer & Jetz 2010; Kisel & Barraclough 2010), incorporates the distances to the nearest mainland, nearest island group and nearest equally sized or larger island. However, nearest landmasses are not necessarily suitable source areas because colonization also depends on the favourability of island environmental conditions, especially on climate (Steinbauer *et al.* 2012). Price (2004) therefore used the distance to the nearest island with analogous habitats as isolation metric.

Moreover, long-distance dispersal depends on dispersal vectors and is influenced by wind and ocean currents (Muñoz *et al.* 2004). To account for this, Diver (2008) used the distance to the nearest upwind landmass. Similarly, Abbott (1974) found the distance to the nearest landmass in a westerly direction to be a strong predictor of plant species richness for a set of islands within the west wind zone of the southern hemisphere.

MacArthur and Wilson (1967) proposed that the spatial arrangement of islands should affect species richness. Stepping stones, i.e. islands located between the source and the target area that are smaller than the source landmass (Gilpin 1980), should facilitate island colonization. Phylogenetic data on various groups of organisms have provided evidence for directional colonization of several archipelagos in the order of island formation (e.g. Garb & Gillespie 2006; Díaz-Pérez *et al.* 2008). In order to account for stepping stones, the shortest over-water distance (Kalmar & Currie 2006) or the largest gap (Diver 2008) along stepping stone paths have been used. Furthermore, the potential for immigration increases with source landmass area (Taylor 1987). In contrast to isolation metrics measured as distances to one specific source, some metrics account for this phenomenon by integrating all landmasses surrounding an island. Weighted by their distances, the areas of surrounding islands sum up to the Neighbour Index by Kalmar and Currie (2006). Accordingly, this and similar metrics (Thornton 1967; Cody 2006) account for island position within an archipelago. Moreover, source landmass geometry is a potentially important factor. Taylor (1987) argued that islands off straight-line shores have higher immigration rates than islands off peninsulas. Source landmass area within defined radii around the target island can thus be quantified to account for coastline shape and the amount of available source area (Diver 2008).

Given the complexity of island isolation in general and the wide variety of ways it has been quantified in particular, it is surprising that no attempts have been made at comprehensive comparisons of isolation metrics at large spatial scales. Here, we revisit island isolation as a central issue in biogeography. We formalize the concepts and metrics just reviewed and supplement them with a series of novel metrics representing different aspects of island isolation. Our objectives are to identify ecologically meaningful metrics and to quantify their relative importance in determining global-scale island biogeographic patterns. We use contemporary vascular plant species richness as response variable, but expect the presented isolation metrics to be relevant also to other biogeographic patterns. We hypothesize that the proportion of variation in species richness explained by isolation can be increased by considering large source islands, stepping stones, climatic similarity, wind and ocean currents and the area of surrounding landmasses, as opposed to considering the distance to the nearest mainland only.

Table II.2.1. Seventeen isolation metrics and their variations analyzed as predictors of vascular plant species richness on a global set of 453 islands. Symbology follows Fig. II.2.1. Metrics and variations indicated by the letter D are true distances measured in kilometres or weighted derivatives; other letters describe dimensionless metrics. References (Ref.): 1. Abbott 1974; 8. Johnson & Simberloff 1974; 3. Case 1975; 2. Abbott 1978; 4. Chown *et al.* 1998; 5. Dahl 2004; 13. Muñoz *et al.* 2004; 14. Price 2004; 7. Hausdorf & Hennig 2005; 12. McMaster 2005; 9. Kalmar & Currie 2006; 6. Diver 2008; 11. Kreft *et al.* 2008; 10. Kisel & Barraclough 2010.

Component	Species pool	Isolation metric	Symbology	Variations / Explanation	Ref.
I. Distance	mainland	distance to nearest mainland	$\mathbf{D1_m}$	a) island mass centroid to coast; b) coast to coast	2, 3, 4, 11
	landmass	distance to nearest landmass	$\mathbf{D2_l}$	varying minimum source area: a-f) 10^0-10^5 km²; g-p) 1-10 times the target island area	8, 12
		UNEP Isolation Index	$\mathbf{U3} = D1b_m^{1/2} + D_a^{1/2} + D2g_l^{1/2}$	D_a = distance to nearest island group or archipelago	5, 10
	climatically similar mainland	distance to nearest climatically similar mainland area	$\mathbf{D4_{cm}}$	-	
	climatically similar landmass	distance to nearest climatically similar landmass area	$\mathbf{D5_{cl}}$	varying minimum source area: a-f) 10^0-10^5 km²	14
II. Stepping stone distance	mainland	stepping stone distance to mainland	${}^{st}\mathbf{C6_m}$; ${}^{st}\mathbf{D6_m} = \sum {}^{ii}D_m$	varying costs in cost distance analysis: a) 1 unit per km over water, 0 units per km over land (${}^{st}\mathbf{D6a_m}$; sum of inter-island distances (${}^{ii}D_m$) in km); b) 2 units per km over water, 1 unit per km over land (${}^{st}\mathbf{C6b_m}$)	9
		stepping stone distance to mainland on minimum inter-island distance path	${}^{stM}\mathbf{C7_m}$; ${}^{stM}\mathbf{D7_m} = (\sum {}^{ii}D_m^x)/y$	a) costs derived from cost distance analysis (${}^{stM}\mathbf{C7_m}$); b-g) unweighted and weighted distances over water extracted from cost distance path (${}^{stM}\mathbf{D7_m}$): b) x = 1, y = 1; c) x = 2, y = 1; d) x = 1, y = ∑ A; e) x = 2, y = ∑ A f) x = 1, y = # g) x = 2, y = #; (x = 2: greater influence of larger distances; y = ∑ A: weighted for area (A) of stepping stones; y = #: weighted for number of stepping stones)	
		maximum inter-island distance between target island and mainland	$\max{}^{ii}\mathbf{D8_m}$	-	6
	landmass (>10^5 km²)	stepping stone distance to landmass	${}^{st}\mathbf{D9_l} = \sum {}^{ii}D_l$	${}^{ii}D_l$ = inter-island distances	7
		stepping stone distance to landmass on minimum inter-island distance path	${}^{stM}\mathbf{C10_l}$; ${}^{stM}\mathbf{D10_l} = (\sum {}^{ii}D_l^x)/y$	a) costs derived from cost distance analysis (${}^{stM}\mathbf{C10_l}$); b-g) unweighted and weighted distances over water extracted from cost distance path (${}^{stM}\mathbf{C10_l}$): b) x = 1, y = 1; c) x = 2, y = 1; d) x = 1, y = ∑ A; e) x = 2, y = ∑ A f) x = 1, y = # g) x = 2, y = #; (x = 2: greater influence of larger distances; y = ∑ A: weighted for area of stepping stones; y = #: weighted for number of stepping stones)	
		maximum inter-island distance between target island and landmass	$\max{}^{ii}\mathbf{D11_l}$	-	
III.Distance modified by wind and ocean currents	mainland	distance to mainland modified by prevailing winds	${}^{W}\mathbf{C12_m}$	-	1, 6, 13
		distance to mainland modified by ocean currents	${}^{C}\mathbf{C13_m}$	-	
IV. Stepping stone distance modified by wind and ocean currents	mainland	stepping stone distance to mainland modified by prevailing winds	${}^{stW}\mathbf{C14_m}$	-	
		stepping stone distance to mainland modified by ocean currents	${}^{stC}\mathbf{C15_m}$	-	
V. Surrounding landmass area	landmass	Neighbour Index	$\mathbf{N16} = \sum (A_l/(D_l + 1)^2)$	a) only islands closer than mainland; b) all islands; c) all landmass; d) all landmass ($\log_{10} A_l$)	9
		proportion of surrounding landmass	$\mathbf{A17_l} = \sum (A_l/A_r)$	a-e) varying buffer radius (r) from 10^0 to 10^4 km (n=1); f-o) sums of landmass proportions in all possible combinations of n=2 to n=5 consecutive buffer distances: f) 10^0-10^1 km; g) 10^1-10^2 km; h) 10^2-10^3 km; i) 10^3-10^4 km; j) 10^0-10^2 km; k) 10^1-10^3 km; l) 10^2-10^4 km; m) 10^0-10^3 km; n) 10^1-10^4 km; o) 10^0-10^4 km	6

Methods

Species richness, geographic reference and abiotic data

In order to evaluate the effects of different aspects of isolation on the species richness of island floras we built on data and statistical models from Kreft *et al.* (2008). These models account for island area, isolation (distance to nearest mainland), topography, climate and geology as predictors of species richness of native vascular plants for a set of 488 islands worldwide. Species numbers were based on a comprehensive review of island floras, checklists and compilations (Text V.2.1). To reduce bias potentially introduced by varying sampling effort and inventory incompleteness (compare Santos *et al.* 2010a), we excluded studies of obvious low quality. However, we acknowledge that even for well-known island floras checklists are rarely complete. To what extent this may influence macroecological analyses at a global scale, cannot be estimated with sufficient accuracy at present. Islands were defined as landmasses smaller than Australia surrounded by ocean. As geographic reference, we used the GADM database of global administrative areas (version 1, Hijmans *et al.* 2009), that contains more than 85,000 high-resolution landmass polygons. For eight islands that could not be assigned to any GADM polygon, a polygon was drawn according to maps in the original publications or digital elevation data at 90 m resolution (Jarvis *et al.* 2008). Large island groups (more than three comparably large islands; e.g. Svalbard) were excluded to avoid issues arising from conceptual differences between single islands and archipelagos. The resulting dataset comprised a global selection of 453 islands, small island groups and atolls (Fig. V.2.1). Island area (km²) as well as latitude and longitude of the mass centroid were calculated for each polygon. Island geology data (continental, volcanic or atoll) were adopted from Kreft *et al.* (2008). Mean annual temperature (°C), annual precipitation (mm a^{-1}) and elevational range (m) were extracted from WorldClim (Hijmans *et al.* 2005). For islands not covered by WorldClim, literature values were taken from Kreft *et al.* (2008). Species richness, area, precipitation, temperature (plus fifty) and elevational range (plus one) were $\log_{10}$-transformed before analysis. GIS analyses were performed in ArcGIS/ArcINFO Desktop 9.3.1 (ESRI, Redlands). Statistical analyses were run in R 2.12.0 (R Development Core Team 2010).

Isolation metrics

We distinguished five isolation components (Table II.2.1): I. Distance, II. stepping stone distance, III. distance modified by wind and ocean currents, IV. stepping stone distance modified by wind and ocean currents and V. surrounding landmass area. These components represent different modes of isolation between a target island and potential species pools. Within the isolation components, we considered different potential source pools: mainland only, all landmasses exceeding a certain minimum area, climatically similar mainland only and all climatically similar landmasses exceeding a certain minimum area. We calculated seventeen conceptually different isolation metrics, with sixty-eight variations in total (Fig. II.2.1 and Table II.2.1) and classified each isolation metric by isolation component and source pool. See Table V.2.1 for a detailed description of the metric calculations and underlying hypotheses. We provide values of twenty-eight metric variations for all 453 islands (Text V.2.2).

I. Distance

All distances were calculated using an azimuthal equidistant map projection centred individually for each target island. We calculated the shortest distance from an island's mass centroid ($D1a_m$) and its coastline ($D1b_m$) to the nearest mainland and the distance from an island's coastline to the nearest landmass exceeding a certain area threshold ($D2_l$). Area thresholds were varied systematically from 10^0 to 10^5 km² and from one to ten times the area of the target island. Distances to climatically similar mainlands ($D4_{cm}$) and landmasses ($D5_{cl}$) were calculated similarly. As sources, we considered areas resembling the climatic space of the target island based on WorldClim (Hijmans *et al.* 2005), i.e. mean annual temperature deviating no more than 2 °C from the range of mean annual temperatures on the target island and annual precipitation being not more than 20% lower than the minimum and not more than 20% higher than the maximum annual precipitation on the target island. These thresholds were chosen arbitrarily to exceed the climatic range of the target island by a reasonable degree. Values of the UNEP Isolation Index (U3) were obtained from the UNEP Island Directory (Dahl 2004) for 229 islands. Missing values were calculated as the sum of square roots of the distances to the nearest equally sized or larger island, the nearest island group or archipelago and the nearest continent (Dahl 2004).

II. Stepping stone distance

We calculated two different types of stepping stone distances, both as the least accumulative cost distances from the nearest source area to a particular target island. Cost distance analysis is a powerful tool in geographical analyses and can, e.g., be used to find the most economic route for a highway through a hilly region. Here, we applied cost distance analysis to estimate the potential immigration pathway between two landmasses crossing a cost surface consisting

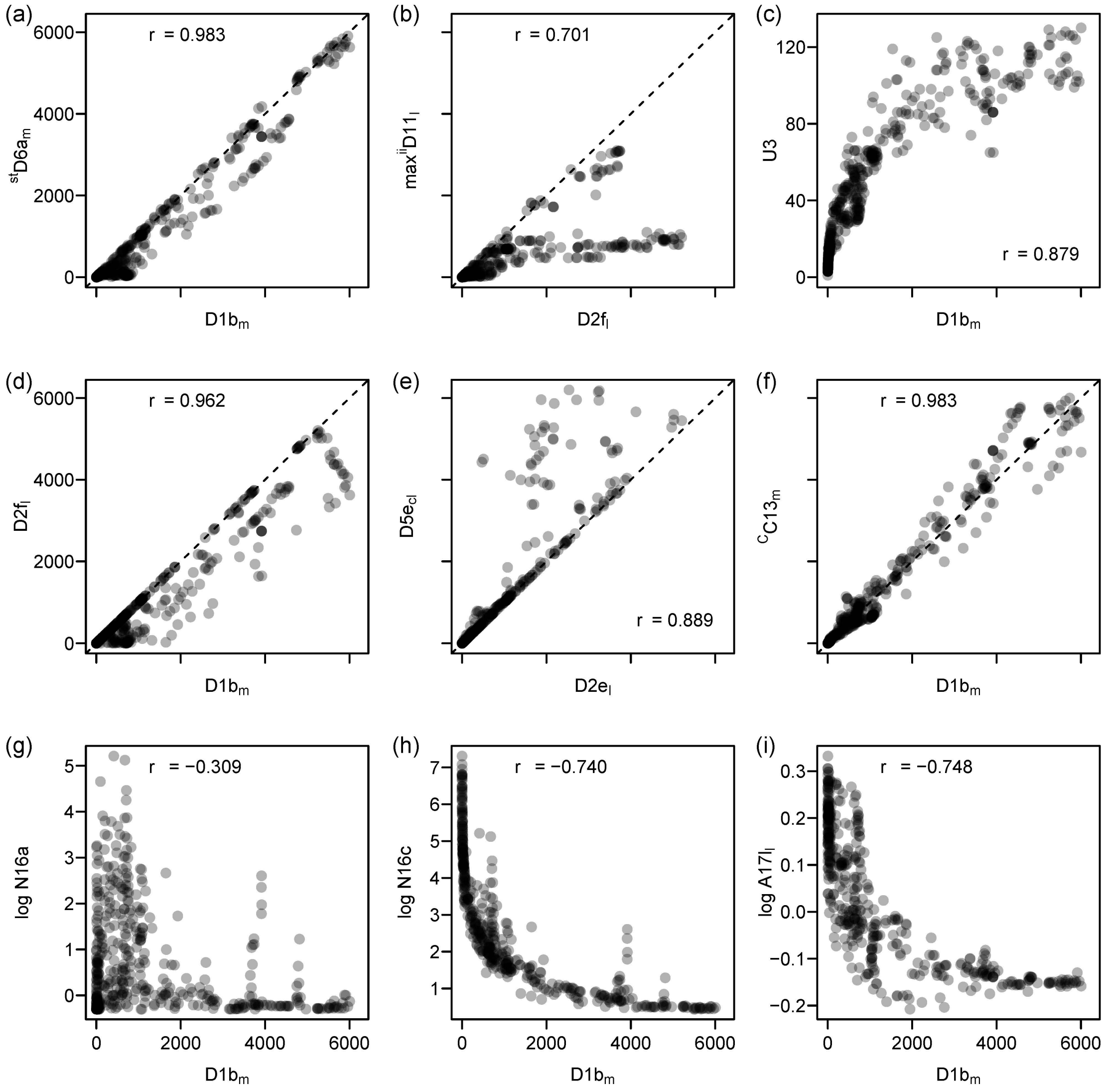

Figure II.2.2. Selected relationships among metrics, illustrating the complexity of quantifying island isolation. All Pearson correlations (r) are significant at $p < 0.001$. Dashed lines indicate isometric lines. Metrics abbreviated with a D are geographic or weighted distances in km. Others are dimensionless. See Fig. II.2.1 and Table II.2.1 for detailed explanation and metric abbreviations.

of open water and potential stepping stone islands. All islands of at least 1 km² were considered as possible stepping stones. First, we minimized the accumulative over-water distance between target island and source area. Costs were defined as either one unit per kilometre over water and zero units per kilometre over land (over-water distance in kilometres) or two units per kilometre over water and one unit per kilometre over land. The source was either defined as the mainland (${}^{st}D6_{m}$) or as a landmass of at least 100,000 km² (${}^{st}D9_{l}$), which was the most important source area size class among the distance to landmass ($D2_{l}$) variations. Second, we computed a stepping stone pathway of minimized inter-island distances by applying costs of one unit per kilometre over land and linearly increasing costs with increasing distance to landmass over water. This was again calculated for mainland (${}^{stM}D7_{m}$) and landmass of at least 100,000 km² (${}^{stM}D10_{l}$) as source area. Area and number of stepping stones were used in the calculation of weighted stepping stone distances. The maximum step length was extracted from the pathway to the nearest mainland (max^{ii}D8$_m$) and the nearest landmass of at least 100,000 km² (max^{ii}D11$_l$).

III. Distance modified by wind and ocean currents

We accounted for wind (^{W}C12$_m$) and ocean currents (^{C}C13$_m$) by incorporating their prevailing directions as horizontal factors in cost distance analyses. Horizontal ocean current directions at the water surface (derived from NASA ECCO2, Menemenlis *et al.* 2008) and wind directions at water and land surfaces (derived from NCEP/NCAR, Kistler *et al.* 2001) were averaged over ten years. Costs were set to one unit per kilometre irrespective of the crossed medium (i.e. land or water).

IV. Stepping stone distance modified by wind and ocean currents

We calculated stepping stone distances considering wind (^{stW}C14$_m$) and ocean currents (^{stC}C15$_m$) as in section III, except that costs were defined as one unit per kilometre over water and zero units per kilometre over land.

V. Surrounding landmass area

We applied two different approaches to assess the effect of surrounding landmasses on the focal islands. The Neighbour Index (N16), proposed by Kalmar and Currie (2006), is the sum of the areas of all surrounding islands closer than the nearest mainland inversely weighted by their squared distances to the focal island. We calculated the Neighbour Index in its original form as well as variations including all islands or all landmasses (raw or log-transformed area). In addition, we computed the proportion of land area in the surrounding of the target island within buffer distances of 10^0 to 10^4 km (A17$_l$). As additional metric variations, we summed up the landmass proportions in all possible combinations of two to five consecutive buffer zones. This metric accounts for the coastline shape of large landmasses by including only the area of the part that extends into a certain buffer.

Statistical analysis

We computed single-predictor regression models with the number of vascular plant species per island ($\log_{10}$-transformed) as the response variable and each isolation metric in turn as the explanatory variable. We then used multi-predictor models including island area, annual mean temperature, annual precipitation, elevational range, geology and one isolation metric variation at a time to assess the explanatory power of each metric variation after accounting for abiotic factors shown to significantly influence species richness on islands (Kreft *et al.* 2008). Best variations of each isolation metric were chosen based on the Akaike Information Criterion (AIC) values of the multi-predictor models. These seventeen best metric variations were used for further analyses. We tested all possible combinations of two or more of these best isolation metric variations in the multi-predictor framework and assessed relative model support using AIC. Pairs of models with $\Delta\text{AIC} < 2$ were considered as receiving equal statistical support (Burnham & Anderson 2002). In order to avoid issues arising from multi-collinearity, we considered only combinations of metrics that were not strongly correlated ($r < 0.7$). Second order interactions between area and isolation metrics were added to the best candidate models including one or more isolation metrics. Non-significant interaction terms were dropped. Isolation metrics entered the analyses both as raw variables and $\log_{10}$-transformed after adding 0.5 to avoid taking the logarithm of zero. Additionally, N16c entered the analyses $\log_{10}$-transformed twice since its frequency distribution was still strongly skewed after the first transformation.

To account for significant spatial autocorrelation in the model residuals of generalized linear models (GLM) we performed spatial simultaneous autoregressive models (SAR) of the error type using the R-package *spdep* (Bivand *et al.* 2011). SARs of the error type model the effect of spatial autocorrelation in the error term by means of a weighted neighbourhood matrix (Bivand *et al.* 2011). This avoids type I error inflation and biased parameter estimates due to autocorrelation (compare Dormann *et al.* 2007). We adopted the neighbourhood structure (lag distance of 1,000 km) and weighting (row-standardization) from Kreft *et al.* (2008), empirically optimized following Kissling and Carl (2008). Patterns of spatial autocorrelation in model residuals were assessed with Moran's I correlograms and global Moran's I values. Applying spatial models significantly reduced spatial autocorrelation in model residuals (Fig. V.2.2) and consistently improved model fits. Results from non-spatial GLMs are shown in Tables V.2.4, V.2.5 and V.2.6. We used GLMs of the Gaussian family because they consistently outperformed GLMs of the Poisson family in terms of model fit (AIC) and model diagnostics (Crawley 2007) in spite of count data as raw response variable. Homoscedasticity and normality of the residuals were evaluated with plots of standardized residuals against fitted values and QQ plots.

Table II.2.2 Model fits of spatial simultaneous autoregressive models (SAR) with the log$_{10}$-transformed number of vascular plant species on 453 islands as response variable and different isolation metrics as explanatory variables. The first model includes no isolation metrics, but only island area, temperature, precipitation, elevational range and geology, and is included for comparison. All other models include one isolation metric, either as a single predictor (r^2) or in a multi-predictor model including also island area, temperature, precipitation, elevational range and geology (R^2). r^2_{sp} and R^2_{sp} accounting for spatial autocorrelation are shown in parentheses. Except for A17l$_l$ and N16c all single predictor relationships are negative. For multi-predictor models, ΔAIC was calculated as the difference from the best model (AIC = 121.8). P-values in the multi-predictor models refer to estimates of the respective isolation metric. R^2_{pmvd} shows the absolute contribution of the respective isolation metric to the full model fit (R^2). See Fig. II.2.1 and Table II.2.1 for metric abbreviations. Significance: *** ($p < 0.001$).

	single-predictor models		multi-predictor models			
Isolation metric	**r^2 (r^2_{sp})**	**p**	**R^2 (R^2_{sp})**	**ΔAIC**	**P**	**R^2_{pmvd}**
-	-	-	0.712 (0.829)	97.0	-	-
D1a$_{m}$	0.240 (0.489)	***	0.786 (0.851)	29.3	***	0.152
D2f$_{l}$	0.264 (0.499)	***	0.786 (0.852)	26.7	***	0.158
U3	0.231 (0.493)	***	0.795 (0.856)	15.9	***	0.151
D4c$_{m}$	0.262 (0.498)	***	0.776 (0.845)	49.8	***	0.111
D5e$_{cl}$	0.299 (0.513)	***	0.800 (0.856)	14.7	***	0.176
st**C6b**$_{m}$	0.253 (0.498)	***	0.786 (0.852)	27.0	***	0.158
^{stM}**D7b**$_{m}$	0.249 (0.492)	***	0.783 (0.849)	35.9	***	0.133
max^{ii}**D8**$_{m}$	0.138 (0.475)	***	0.778 (0.845)	49.8	***	0.074
st**D9**$_{l}$	0.264 (0.497)	***	0.793 (0.852)	24.4	***	0.161
^{stM}**D10b**$_{l}$	0.230 (0.485)	***	0.778 (0.848)	37.8	***	0.122
max^{ii}**D11**$_{l}$	0.180 (0.483)	***	0.777 (0.845)	48.4	***	0.096
^{W}**C12**$_{m}$	0.254 (0.503)	***	0.763 (0.846)	44.8	***	0.123
^{C}**C13**$_{m}$	0.251 (0.501)	***	0.782 (0.851)	28.6	***	0.152
^{stW}**C14**$_{m}$	0.273 (0.502)	***	0.775 (0.849)	34.8	***	0.146
^{stC}**C15**$_{m}$	0.253 (0.499)	***	0.787 (0.853)	22.3	***	0.163
loglog **N16c**	0.253 (0.514)	***	0.786 (0.852)	28.9	***	0.151
log **A17l**$_{l}$	0.185 (0.479)	***	0.807 (0.861)	0.0	***	0.134

We calculated pseudo-R^2 values for SAR models as the squared Pearson correlation coefficients between fitted and observed values (Kissling & Carl 2008). For non-spatial models, the pseudo-R^2 equals the ordinary least squares R^2. Fitted values of SAR models can be partitioned additively into trend (non-spatial smooth) and signal (spatial smooth). We calculated both a pseudo-R^2 for the fitted values including the spatial component (hereafter R^2_{sp}), and a pseudo-R^2 for the trend excluding the spatial component, which represents the part of the variation explained by the predictors (in the context of SAR models hereafter R^2).

We calculated the relative importance of each isolation metric in the multi-predictor models using the metric 'pmvd' in the R-package *relaimpo* (Grömping 2006). The 'pmvd' calculates a weighted average of sequential R^2-values over all possible models. To account for spatial autocorrelation, we calculated SAR models and removed the spatial signal of the fitted values from the response variable. Log-transformed species richness excluding the spatial signal entered the calculations of relative importance as response variable in linear models (Belmaker & Jetz 2011). We multiplied the obtained relative proportions (hereafter proportional R^2_{pmvd}) by the SAR model R^2 values in order to get the absolute fraction of the multi-predictor R^2 explained by a particular variable (hereafter R^2_{pmvd}).

To analyze potential interactions between isolation and other predictors, we calculated sequences of 303 multi-predictor models along all islands ordered by area, temperature, precipitation, or elevational range, using data subsets comprising one third of the islands each, e.g. starting with the 151 smallest and ending with the largest islands. In order to show the relative importance of the isolation metrics along the environmental gradients, we calculated the proportional R^2_{pmvd}. 95% confidence intervals of a null model for 151 randomly selected islands were calculated from 1,000 permutations. Relative importance of the isolation metrics within geologic subsets was calculated and compared to null models accordingly.

Results

Patterns of isolation

The islands studied represent a wide range of isolation. Distance to the mainland ($D1b_m$) ranged from less than 100 m (Curtis Island, Australia) to more than 6,000 km (e.g. Rapa Iti, French Polynesia; median = 663.1 km). The various isolation metrics show a high degree of collinearity. While some metrics were perfectly correlated, others were less closely related (lowest correlation: $max^{ii}D8_m$ and $^{W}C12_m$, r = 0.55; Table V.2.2). The relationships among some metrics are governed by simple geometric constraints (Fig. II.2.2). For example, simple stepping stone distances ($^{st}D6_m$, $^{st}D9_l$, $max^{ii}D8_m$, $max^{ii}D11_l$) can only be shorter than or equal to the respective straight-line distances ($D1_m$, $D2_l$; Fig. II.2.2a-b). The same holds true for distances to a landmass ($D2_l$, $D5_{cl}$, $^{st}D9_l$, $^{stM}D10_l$) compared to distances to the mainland (Fig. II.2.2d). In contrast, distances to climatically similar areas can only be equal to or longer than distances disregarding climatic similarity (Fig. II.2.2e). Distances taking into account wind or ocean currents may be shorter or longer than simple straight-line distances, while deviations from straight distances increase with distance (Fig. II.2.2f). Metrics accounting for the landmass area surrounding an island (N16, $A17_l$) are nonlinearly and less strongly related to distance metrics (Fig. II.2.2g-i).

Best metric variations

For each isolation metric, we identified the best variation according to the spatial multi-predictor model AIC (Table II.2.2; see Table V.2.3 for SAR model results for all metric variations). The distance from the island coast to the mainland coast ($D1b_m$) did not perform better than the respective distance from the mass centroid ($D1a_m$). Model fits of the distance to a source landmass improved with increasing minimum area thresholds of the landmass, reaching a maximum at 100,000 km^2 for the minimum area of any landmass ($D2f_l$) and 10,000 km^2 for climatically similar landmasses ($D5e_{cl}$; Fig. II.2.3a). The distance to a landmass of a certain minimum size defined as a multiple of the target island area did not gain strong statistical support ($D2g_l$ - $D2p_l$). The stepping stone distance on a minimum inter-island distance path was best represented by the length of the path itself (${}^{stM}D7b_m$, ${}^{stM}D10b_l$). Weighting of the path length by the number or area of the stepping stones did not improve model fits. The original Neighbour Index did not contribute considerably to explaining species richness (log N16a). However, the double log-transformed version of its variation accounting for all kinds of landmass performed significantly better (loglog N16c). The sum of the proportions of landmass within a buffer distance of 100 km, 1,000 km and 10,000 km ($A17l_j$) was the best metric variation of $A17_l$. The best variation considering the proportion of landmass within only one buffer zone used a radius of 1,000 km (Fig. II.2.3a).

Species richness models

Clear differences emerged from a comparison of the seventeen selected isolation metrics. Distances to landmasses yielded higher multi-predictor model fits than distances to the mainland (Table II.2.2). This pattern was consistent across ordinary distances, distances accounting for climatic similarity and simple stepping stone distances. Simple stepping stone distances performed better than ordinary distances irrespective of the source landmass and whether wind or ocean currents were corrected for or not. Length and costs of the minimum inter-island distance path as well as the minimum inter-island distance did not yield strong statistical support. Consideration of prevailing winds did not improve model fits. Models accounting for ocean currents performed better than models based on unweighted distances when stepping stones were considered. The modified Neighbour Index (N16c) did not improve the model fit compared to the distance to mainland.

The overall best metric in a multi-predictor framework was the proportion of surrounding landmass, log $A17l_l$ (AIC = 121.8; Fig. II.2.3e, Table II.2.2). This model explained 86.1% of the variation. However, its contribution to overall R^2 measured as R^2_{pmvd} was comparatively small ($R^2_{pmvd} = 0.134$) due to a weak single-predictor relationship of the metric and species richness (Fig. II.2.3b). Second best models according to AIC included the distance to climatically similar landmass ($D5e_{cl}$) and the UNEP Isolation Index (U3; Fig. II.2.3d & f). The strongest single-predictor relationship ($r^2 = 0.299$) and relative importance ($R^2_{pmvd} = 0.176$) were found for $D5e_{cl}$ (Fig. II.2.3c). These results are consistent with results from non-spatial models (Table V.2.4).

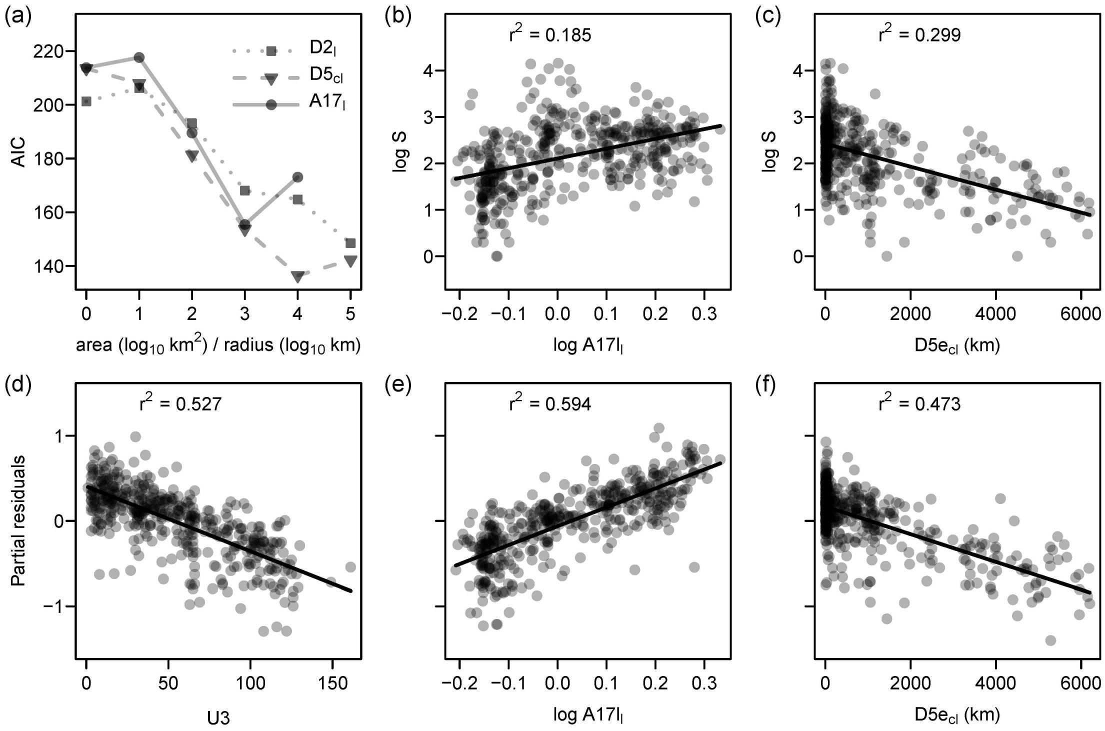

Figure II.2.3. Selected relationships between the $\log_{10}$-transformed number of vascular plant species on 453 islands worldwide (log S) and different island isolation metrics. (a) Model fit (AIC) of spatial multi-predictor models including one metric variation of D2$_l$, D5$_{cl}$, or A17$_l$ and five other core predictors of island richness (area, temperature, precipitation, elevational range, geology). Metric variations differ in the minimum area of the considered potential source landmass (D2$_l$, D5$_{cl}$) or the radius of the buffer in calculations of surrounding landmass proportions (A17$_l$). Note that lower AIC values indicate higher relative model support. (b-c) Simple linear relationships. (d-f) Partial residual plots for the three isolation metrics that produced highest model fits in the multi-predictor framework. The plots show the individual effects of the isolation metrics after effects of other predictors and spatial autocorrelation have been partialled out. See Fig. II.2.1 and Table II.2.1 for metric abbreviations.

Including more than one isolation metric in the multi-predictor models significantly improved model fits (Table V.2.5). The model with the lowest AIC (81.5) included the proportion of surrounding landmass (A17l$_l$), the distance to climatically similar landmass (D5e$_{cl}$) and the maximum inter-island distance (max^{ii}D11$_l$). These metrics represent three different components of isolation, two different source pool concepts (Table II.2.1), and are only moderately collinear ($r < 0.7$; Table V.2.2). Models including four isolation metrics did not perform better in terms of AIC. Adding second-order interactions between area and the three isolation metrics included in the best model further improved the model fit (AIC = 56.15 after dropping the non-significant interaction between log-area and max^{ii}D11$_l$). Isolation was the second most important factor explaining species richness in all compared candidate models, explaining up to 23% of the variation in species richness. Only area showed a higher relative importance (Table V.2.5).

Species richness correlates in environmental subsets

Species richness correlates of the strongest isolation metrics showed similar trends for island subsets along environmental gradients (Fig. II.2.4). However, the effect of distance metrics on species richness was generally strongest for medium-sized islands, whereas the maximum influence of surrounding landmasses ($A17j_l$) was seen in small islands (Fig. II.2.4a), contributing up to 60% of the explained variation. The contribution of all considered metrics decreased rapidly when including large islands (>1,000 km^2). The relative importance of isolation decreased with increasing mean annual temperature (Fig. II.2.4b). Maximum contribution to explaining species richness, for all metrics, was found for low to medium annual precipitation and medium elevational range (Fig. II.2.4c & d). Isolation was a much weaker correlate of species richness for continental than for oceanic islands and for volcanic islands than for atolls (Fig. II.2.4e). Distance to climatically similar landmass ($D5_{cl}$) was the most important metric for species richness on atolls. For other geologic categories no considerable differences among isolation metrics were found.

Discussion

We present the first comprehensive, comparative analysis of island isolation with broad geographic extent. The only other comparison of a wide variety of isolation metrics we are aware of was presented by Diver (2008), studying the relationship between isolation and richness of vascular plants on near-shore freshwater islets. We confirm previous findings that isolation is a strong predictor of species richness (e.g. Kalmar & Currie 2006). Single isolation metrics explained up to 17.6% of the variation in vascular plant diversity (distance to nearest climatically similar landmass area, $D5e_{cl}$; Table II.2.2). However, our study emphasizes that a variety of facets of isolation affect island colonization and the maintenance of established populations. Importantly, not a single metric alone accounted for all the variation. Rather, different aspects contributed to defining isolation as a driver of species richness.

Our results demonstrate that proximity to neighbouring large islands is an important driver of island species richness ($D2f_l$, $D5e_{cl}$; Table II.2.2). This suggests that large islands, as well as continents, serve as major sources for colonization and maintenance of species richness. We also show that the absolute area of a potential source is more important than its size relative to the target island ($D2g\text{-}p_l$; Table V.2.3). This lines up with theoretical expectations, as numbers of potentially immigrating species and propagules both increase with source area (MacArthur & Wilson 1967). Small islands are therefore less important sources of immigration, even for small target islands (Fig. II.2.3a). However, the potential of a source depends on the island of interest and colonization depends on favourable environmental conditions (MacArthur & Wilson 1967; Steinbauer *et al.* 2012), making it more likely that islands receive colonizers from climatically similar areas. Additionally, continental refugia provide evidence that climatic barriers may modify isolation influencing migration and diversification (Willis & Whittaker 2000; Médail & Diadema 2009). To our knowledge, climate has not been considered in measurements of island isolation before, although it is clearly an important factor at a global scale. This hypothesis is supported by the strength of our metric using the distance to climatically similar landmasses ($D5e_{cl}$; Table II.2.2). It is noteworthy that this simplistic metric significantly improved the fit of species richness models.

We found the strongest effect of isolation when measuring the proportion of surrounding landmass ($A17l_{l}$, Fig. II.2.3e), a metric that incorporates the distance to large landmasses, their area and their coastline shape (Fig. II.2.1). This finding is consistent with Diver (2008) and indicates that not only the distance to but also the amount of available source area drives immigration rates. At a global scale, the proportion of landmass within large buffer distances (100 - 10,000 km) were most important (Fig. II.2.3a) highlighting the relevance of an island's position relative to very large landmasses. However, Diver's (2008) results, in which species richness was best explained by the landmass proportion within a 0.25 km buffer, suggest that the optimal buffer radius for measuring isolation depends on the spatial scale of the study.

The fact that stepping stone metrics consistently gained higher statistical support than straight distances (Table II.2.2) strongly suggests that direct dispersal is not the only relevant immigration mechanism. Instead, it indicates that islands between target and source areas decrease isolation, and supports the hypothesis that island-hopping is an important mechanism (Whittaker & Fernández-Palacios 2007). For instance, spatially clustered island groups along edges of tectonic plates or above volcanic hotspots, such as the Kuriles or the Canaries, may make dispersal possible to islands far off the mainland for species not capable of extraordinary long-distance dispersal (compare Fig. 1a in Fernández-Palacios *et al.* 2011). When accounting for the two strongest metrics ($D5e_{cl}$ and $A17l_{l}$), the maximum inter-island distance ($max^{ii}D11_{l}$) emerged as a significant predictor (Table V.2.5). The variation additionally explained by $max^{ii}D11_{l}$ might be attributed to species with restricted long-distance dispersal abilities, for which the chance of immigration depends on the maximum distance to cross.

We did not find consistent support for metrics including prevailing wind and ocean currents although these factors are assumed to strongly affect dispersal (Muñoz *et al.* 2004; Cook & Crisp 2005). We used ten-year means of zonal and horizontal velocities for the calculation of prevailing directions, which blurred seasonality. Generally, rare extremes, such as tropical cyclones, are expected to support long-distance dispersal (Bullock & Clarke 2000). In contrast,

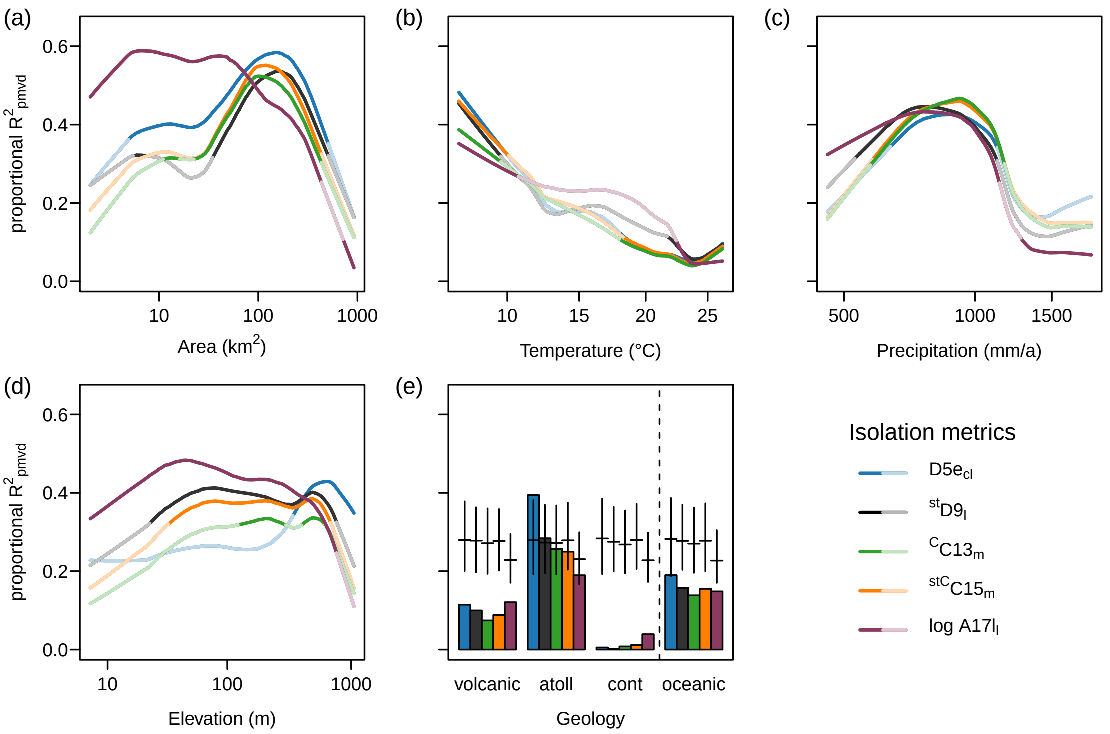

Figure II.2.4. Interactions between isolation metrics and other core predictors of island richness. (a-d) Relative importance (proportional R^2_{pmvd}) of the best isolation metrics among five isolation components shown for sequences of data subsets including one third of the entity of 453 islands. Proportional R^2_{pmvd}-values were calculated based on simultaneous autoregressive models (SAR) of vascular plant species richness accounting for area, temperature, precipitation, elevational range, geology and the respective isolation metric. The data subsets were consecutively taken from the full dataset ordered by (a) area, (b) temperature, (c) precipitation and (d) elevation. X-axes in (a-d) are shown in $\log_{10}$-scale and give the median values of the sorting variables. Parts of the lines not significantly different ($p < 0.05$) from random draws of the same number of islands are shown in light shades. (e) Proportional contribution to overall R^2 of isolation for islands of different geologic origin (oceanic islands comprise volcanic islands and atolls, cont - continental islands). Null model median and 95% confidence intervals are indicated by black lines. See Fig. II.2.1 and Table II.2.1 for metric abbreviations.

Tackenberg *et al.* (2003) argued that low horizontal wind speeds enhance the dispersal potential. However, currents may change drastically over the relevant time scales of island emergence and colonization. Present day conditions might therefore be weak predictors of past immigration events (Ali & Huber 2010; Fernández-Palacios *et al.* 2011). Our results suggest that currents in general and ocean currents in particular ($^{stC}C15_m$; Table II.2.2) can affect insular species richness. But due to methodological constraints, we are careful to draw final conclusions.

Another potential source of uncertainty is the similarity of some of our isolation metrics: the presented metrics showed a considerable degree of collinearity (Table V.2.2). Their similarity made differences in their predictive power appear small and hampered direct inferences about their relative importance and biogeographic role. However, our results were consistent among different models, highly collinear metrics were not included in single models, and metric comparisons were based on model fit, which should be independent of collinearity (Graham 2003).

Another factor to consider in interpreting our results is that isolation effects may interact with species-specific dispersal properties (Lomolino 1982). Water-dispersed species should be affected by ocean currents, whereas winds should strongly affect wind-dispersed species. Stepping stones could be of particular importance for dispersal by birds and of minor importance for species passively dispersed by wind or water (MacArthur & Wilson 1967). Isolation in general may be of minor importance for species with very light, wind dispersed diaspores, such as ferns, which are relatively speciose on islands (Kreft *et al.* 2010; but see Vargas *et al.* 2012). Our analysis for vascular plants can only provide a generalized picture, but future comparative studies could shed light on trait-specific patterns.

Just as indicated for wind and ocean currents, our correlative approach in general was limited by the fact that the explanatory variables tested represented only contemporary conditions (compare McGlone 1996). We did not include historical isolation (compare Hausdorf & Hennig 2005) or island age due to a lack of data. Hence, we had to disregard important factors such as the developmental state of islands, the elapsed time available for cladogenesis and changing isolation scenarios due to sea level changes, volcanism and tectonic drift. We show that contemporary isolation is more important for oceanic than for continental islands (Fig. II.2.4e) possibly reflecting connections of continental islands to continents in the past (Whittaker & Fernández-Palacios 2007). In addition, oceanic islands show varying rates of immigration, speciation and extinction over time when emerging through volcanic activity or submerging by erosion (Whittaker *et al.* 2008). On a geologic time scale, they are relatively ephemeral landmasses. Stepping stone metrics, for instance, might therefore be biased as a result of ignoring submerged islands that were crucial for past immigrations (for reconstruction of, e.g., Palaeo-Macaronesia see Fernández-Palacios *et al.* 2011). Furthermore, not only may the isolation from a proper source pool change, but also the properties of the source itself (e.g. total number of species, potential colonizers) may be subject to significant changes over relevant times due to geologic and climatic changes (Fernández-Palacios *et al.* 2011; Zobel *et al.* 2011). Given these inevitable limitations, it is remarkable that our models explained up to 87% of the variation in vascular plant species richness and that the additive effects of three metrics of contemporary isolation contributed 23% (Table V.2.5).

Despite not having included evolutionary processes in our analysis, we can infer that cladogenesis on large islands may counteract the negative effect of isolation on species richness. The probability of speciation increases with area (Heaney 2000; Kisel & Barraclough 2010). Given enough time, large isolated islands should approach their carrying capacity via cladogenesis even if colonization events are rare (Whittaker *et al.* 2008). Isolation is therefore expected to be less important for species richness on very large islands, which was confirmed by our subset analysis (Fig. II.2.4a). Small to medium-sized islands that hold unstable populations, however, could be affected considerably by isolation. Due to source and sink dynamics (Pulliam 1988) and complex metapopulation systems (Hanski & Gilpin 1991), species on small and less isolated islands consist partly of populations that are not viable without steady immigration of individuals ('rescue effect', Brown & Kodric-Brown 1977). Accordingly, we found that particularly the proportion of surrounding landmass area ($A17l_l$) has a great influence on species richness on small islands (Fig. II.2.4a) possibly via its negative effects on extinction rates. In addition to area, temperature and precipitation influenced isolation effects on species richness (Fig. II.2.4b & c). This suggests that isolation might be more important on islands where overall carrying capacity is low due to low productivity (Wright 1983) and where cladogenesis is less likely due to low temperatures (Allen *et al.* 2002). Besides area and climate, elevational range (as surrogate of environmental heterogeneity) influenced the effect of isolation on species richness (Fig. II.2.4d). On heterogeneous, isolated islands, cladogenesis may be promoted by a comparatively empty niche space (Heaney 2000). Furthermore, diversification rates can be expected to increase with altitude due to a greater climatic isolation of high elevation ecosystems (Steinbauer *et al.* 2012). Our results add to this by showing a decrease of the influence of isolation on richness with increasing elevational range for the proportion of surrounding landmass area ($A17l_l$; Fig. II.2.4d).

We conclude that isolation is comprised of multiple components that cannot be captured in a single metric. In fact, a range of different immigration mechanisms influence island biogeographic patterns. The ordinary distance to the nearest mainland is an adequate and simple-to-calculate measure. However, accounting for stepping stones, large islands as source areas, climatic similarity and the area of surrounding landmasses increases the explanatory power of isolation for species richness. At a global scale, the proportional landmass within certain buffer distances around an island is the best metric ($A17l_l$). The effect of isolation depends on the degree of isolation of the considered system and the dispersal mode of the studied taxa (Lomolino 1982) as well as on abiotic factors. We therefore suggest choosing metrics for a study system on an empirical basis. The provided metrics (Text V.2.2) may be useful not only in analyses of species richness but also of other biogeographic patterns such as gene flow and genetic diversity (Slatkin 1993), speciation (Kisel & Barraclough 2010), endemism (Bunnefeld & Phillimore 2012), phylogeography (Cook & Crisp 2005), species composition and turnover (Hausdorf & Hennig 2005), community structure (Santos *et al.* 2011) or species traits (Meiri *et al.* 2005). Finally, it would be useful to test the isolation metrics in other isolated or fragmented systems.

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Chapter II.3

Biogeographic, climatic and spatial drivers differentially affect alpha, beta and gamma diversity in oceanic archipelagos

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Abstract

Analyses of island biodiversity largely ignore the spatial setting within archipelagos. Here, we assessed the differential effects of intra-archipelagic spatial structure (archipelago area, number of islands, area range, connectivity, environmental volume, inter-island distance), biogeographic factors (area, isolation, age, elevation), and current and past climate (temperature, precipitation, seasonality, climate change velocity) on plant diversity in 23 archipelagos worldwide. We additively partitioned species diversity of each archipelago (γ) into α, β, nestedness and replacement β-components to investigate the relative importance of environmental and spatial drivers. Multiple regressions revealed strong effects of biogeography and climate on α and γ whereas spatial factors, particularly inter-island distance and area range, were key to explain β. Structural equation models confirmed these effects on α and β, but suggested that γ is predominantly determined by indirect abiotic effects via its components, particularly β. Our framework can be applied more widely to other taxa and other archipelago-like systems.

Introduction

The origin and maintenance of island biodiversity is of key interest in ecology, biogeography, and evolution (MacArthur & Wilson 1963; Whittaker & Fernández-Palacios 2007; Losos & Ricklefs 2009). Islands are ideal study systems because they are comparatively small, have distinct boundaries, and their biotas are usually less complex than those on adjacent continents. Many isolated islands and archipelagos exhibit striking examples of evolutionary diversification (e.g. Mayr 1963; Losos & Ricklefs 2009). Consequently, island research has made essential contributions to our understanding of key ecological and evolutionary processes including immigration and extinction (MacArthur & Wilson 1963), speciation and adaptive radiation (Gillespie & Roderick 2002; Losos & Ricklefs 2009; Kisel & Barraclough 2010), founder effects and genetic drift (Grant 1998), and taxon cycles (Ricklefs & Bermingham 2002).

Most previous studies have related biogeographic and climatic island characteristics to patterns of species richness and endemism (Whittaker & Fernández-Palacios 2007; Kreft *et al.* 2008; Lomolino *et al.* 2010b). The seminal equilibrium theory of island biogeography by MacArthur and Wilson (1963) emphasized the role of area and geographical isolation as key factors for community assembly and species numbers on islands. More recently, the importance of time for insular biodiversity dynamics has been highlighted, especially for oceanic islands (Whittaker & Fernández-Palacios 2007; Losos & Ricklefs 2009; Lomolino *et al.* 2010b). These dynamic models of species richness on islands emphasize that diversity not only depends on area and isolation, but also on the age and the geological ontogeny of islands and the associated changes in ecological conditions (Heaney 2000; Whittaker *et al.* 2008; Rosindell & Harmon 2013). Finally, strong effects of other environmental determinants such as modern macroclimate, elevation and habitat heterogeneity have also been shown to influence insular biodiversity (Kadmon & Allouche 2007; Kreft *et al.* 2008; Hortal *et al.* 2009).

Common to most studies on determinants of island biodiversity is their focus on individual islands as the unit of analysis, disregarding their spatial organization within archipelagos. To date, species diversity within archipelagic settings has been studied for only a limited number of iconic archipelagos such as the Canaries, Azores, Hawaii, or Galapagos (e.g. Emerson & Kolm 2005; Hortal *et al.* 2009; Chiarucci *et al.* 2010). This small number of well-studied archipelagos has so far precluded robust statistical analyses on the role of intra-archipelagic variables on island biodiversity (Chiarucci *et al.* 2010). Nevertheless, there is evidence that the spatial structure of islands within archipelagos plays a major role in shaping the evolutionary distinct biodiversity of islands and archipelagos, e.g. via speciation and adaptive radiations (Losos & Ricklefs 2009) or dispersal and taxon-cycle dynamics (Ricklefs & Bermingham 2002). Moreover, the number of species on an island not only depends on the island's distance to the mainland but also on the availability of stepping stones and the amount of landmass in the surroundings (Weigelt & Kreft 2013). Consequently, isolation and inter-island connectivity also need to be considered within archipelagos as proxies for the intra-archipelagic spatial structure.

Integrating the intra-archipelagic spatial arrangement of islands into an analysis not only requires the quantification of new sets of environmental factors (Weigelt *et al.* 2013a), but also the consideration of an intra-archipelagic scale, which can be extended to diversity data. For instance, it is important to quantify the species diversity of individual islands (α) and the differences among islands (β) that result in the species diversity of the entire archipelago (γ). Furthermore, β can be partitioned into nestedness (β_{nst}) and replacement (β_{rpl}) components to quantify the nestedness and dissimilarity across sites (Baselga 2012). For archipelagos, it has been shown that the relative proportions of α, β_{nst}, and β_{rpl} can considerably vary across space (Chiarucci *et al.* 2010). However, it remains unclear to what extent abiotic factors related to archipelagic environment, geology, or intra-archipelagic structure might differentially affect these diversity components.

Biogeographic, climatic and spatial factors may play differential roles in influencing the components of archipelagic diversity. Insular and continental studies suggest that α is strongly

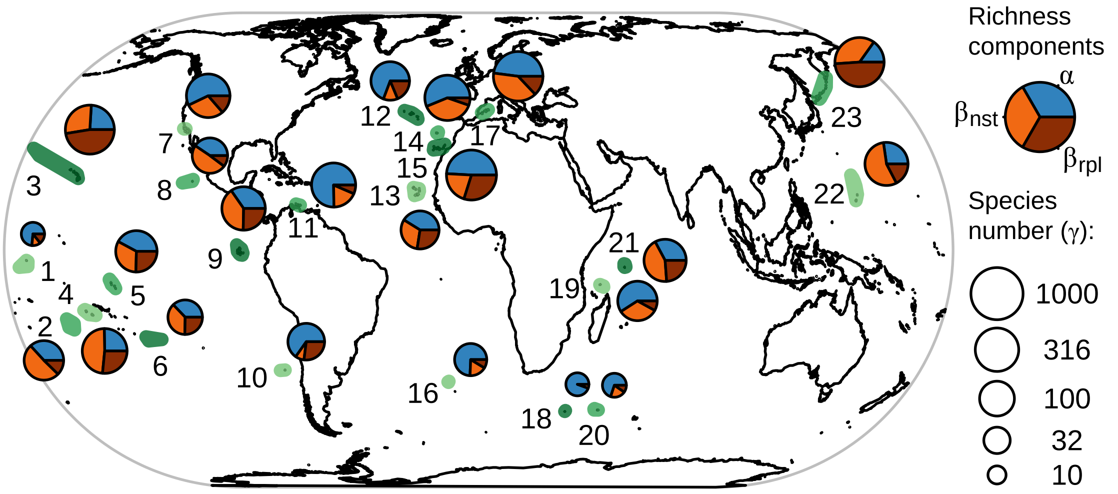

Figure II.3.1. Species richness (γ) of vascular plants on 23 oceanic archipelagos worldwide, additively portioned into α, nestedness (β_{nst}), and replacement (β_{rpl}) components. Circle sizes indicate the total number of species in the archipelago (γ), whereas the colored slices indicate the relative contribution of α, β_{rpl} and β_{nst} to γ. Note that β_{rpl} and β_{nst} add up to β_A as used throughout the manuscript. A detailed description of the calculation of diversity components is provided in the Methods section. Archipelagos are highlighted in green shades and numbered: 1- Phoenix Islands; 2- Cook Islands; 3- Hawai'i; 4- Society Islands; 5- Marquesas; 6- Pitcairn Islands; 7- Northern Californian Channel Islands; 8- Revillagigedo Islands; 9- Galapagos Islands; 10- Juan Fernandez Islands; 11- Dutch Caribbean; 12- Azores; 13- Cape Verde; 14- Madeira; 15- Canary Islands; 16- Tristan da Cunha; 17- Balearic Islands; 18- Prince Edward Islands; 19- Aldabra; 20- Crozet Islands; 21- Inner Seychelles; 22- Marianas; 23- Kuril Islands.

affected by area and local scale environmental heterogeneity (e.g. Kallimanis *et al.* 2008), whereas β is strongly driven by large-scale environmental heterogeneity (e.g. Freestone & Inouye 2006; Veech & Crist 2007) and spatial landscape structure (Fahrig 2003; Diekötter *et al.* 2008). Considering that γ diversity results from both its α and β components, potential abiotic drivers may actually affect γ indirectly via α and β rather than directly (Stegen *et al.* 2013). Spatial intra-archipelagic structure may be important for γ diversity because of its effects on the β component, namely species turnover among individual islands. Hence, the intra-archipelagic spatial structure could have an indirect effect on γ diversity via its β component. However, it is reasonable to assume that biogeography (e.g. isolation and area) and climate (e.g. temperature) still affect archipelagic γ diversity directly, as has been recently suggested for breeding birds at a continental scale (Stegen *et al.* 2013).

Here, we provide a first global assessment of determinants of α, β, β_{nst}, β_{rpl}, and γ diversity on oceanic archipelagos. In contrast to previous studies, we incorporate spatial variables besides classic biogeographic and climatic factors. We test to what extent variables describing the internal spatial structure of archipelagos (connectivity, number of islands, mean inter-island distance, etc.) affect α, β, β_{nst}, β_{rpl} and γ relative to biogeographic (area, isolation, age) and climatic drivers. Additive diversity components were computed from an occurrence dataset of nearly 9,000 vascular plant species on 174 islands belonging to 23 archipelagos worldwide. Specifically, we tested three hypotheses: H1) α is mainly related to biogeographic (e.g. area, isolation, age) and climatic (e.g. temperature, precipitation) determinants; H2) β is mainly driven by intra-archipelagic spatial structure, with differential effects of island arrangement (e.g. inter-island distance, connectivity) on β_{nst} and β_{rpl}; H3) γ is mainly driven by indirect effects, i.e. through biogeographic, climatic and intra-archipelagic drivers that act via the α and β components on *γ* diversity. Overall, we demonstrate that intra-archipelagic spatial variables are key to understand patterns of species diversity on oceanic archipelagos, in addition to biogeographic and climatic determinants.

Methods

Diversity data

We assembled a comprehensive vascular plant database for 174 islands belonging to 23 oceanic archipelagos worldwide (see Table V.3.1 for archipelagos and related literature sources; island-level data can be accessed at Dryad: dx.doi.org/10.5061/dryad.3jv54). This database includes presences of a total of 8,856 native vascular plant species. The archipelagos cover a wide range of climate zones, ocean basins and environmental characteristics (Fig. II.3.1). For each archipelago, we considered all islands >1 km^2. Islands that geologically belong to a neighbouring larger island or to an atoll were merged with those and three islands with missing climate data were excluded (see Table V.3.1).

We followed the additive diversity partitioning approach of Chiarucci *et al.* (2010) to partition the diversity of an entire archipelago (γ) into α and β components (in the following referred to as βA due to its additive nature, following Tuomisto 2010). From the species lists, we obtained the total number of species per archipelago (γ) as well as the number of species for each island and derived the α component for each archipelago as the mean species richness of the single islands within the archipelago. We calculated β_A ('absolute species turnover' sensu Tuomisto 2010) by subtracting α from γ. We further partitioned β_A into replacement (β_{rpl}) and nestedness (β_{nst}) components (sensu Chiarucci *et al.* 2010; see also Baselga 2010b, 2012). The β_{nst} component is given by $(\sum S_{max} - S_i)/N$, where S_{max} is the number of species of the most species-rich island, S_i the number of species of the island i within the archipelago, and N the number of islands in the archipelago. Consequently, β_{nst} is the mean deviance of S_i from S_{max} and equals $S_{max} - \alpha$. Following Chiarucci *et al.*(2010), we retained the term ‘nestedness’, although β_{nst} was not calculated based on species identities and thus deviates from other concepts of nested assemblages (Baselga 2012). The β_{rpl} component is then simply $\beta_A - \beta_{nst}$, representing the part of β_A that cannot be explained by sole differences in species richness among islands. All diversity components were measured in species number, and thus can be also referred as species richness. The measured diversity components were strongly correlated (Pearson’s $r \geq 0.77$; Table V.3.2), as expected due to the additive partitioning (Baselga 2010a; Anderson *et al.* 2011). Consequently, we additionally calculated ratios for β_A/α ('Whittaker's species turnover' or $\beta Mt-1$, sensu Tuomisto 2010) and β_{rpl}/β_{nst}. The advantage of these ratios is that they are mathematically independent of γ. We further calculated a regional-to-local diversity ratio γ/α (also known as ‘Whittaker's beta diversity’ or ‘multiplicative beta’, Tuomisto 2010), but this measure was highly correlated with β_A (Pearson's $r = 0.74$) and with the β_A/α ratio (Pearson's $r = 0.96$) and was thus excluded from the analyses.

Abiotic data

For each archipelago, we assembled a total of fifteen abiotic predictor variables representing three categories: four classic island biogeographic (*BioGeo*), five present and past climatic (*Clim*), and six intra-archipelagic spatial (*IntraArch*) variables.

The four island biogeographic variables were island area (in km^2), surrounding landmass proportion (unitless), age of the oldest island (in million years), and maximum elevation (in m). Island area was calculated as the planar land area. As a measure of island isolation, we used surrounding landmass proportion, which is an inverse proxy for isolation from a hypothetical source pool and a strong predictor of the number of plant species on islands worldwide as it accounts also for coastline shape and neighbouring islands. We calculated the proportion of landmass in buffer distances of 100, 1,000, and 10,000 km around the perimeter of each archipelago (ArcGIS version 9.3.1., ESRI, Redlands, USA). Proportions were summed up and the sum was $\log_{10}$-transformed after adding 0.5 as a constant (Weigelt & Kreft 2013). For archipelago age, we collected the age of the oldest island per archipelago (in million years) from the literature (Table V.3.3). Island age gives an estimate of time for colonization and speciation (Whittaker *et al.* 2008). Finally, elevation was quantified as the maximum elevation within an archipelago and obtained from Weigelt *et al.* (2013a). This measure is commonly used to represent habitat heterogeneity within single islands (e.g. Kreft *et al.* 2008).

The five climatic variables were annual mean temperature (in ˚C), annual precipitation (in mm year^{-1}), annual range in temperature (in ˚C, as a measure for temperature seasonality), the coefficient of variation of precipitation (unitless, as a measure for precipitation seasonality), and Late Quaternary climate change velocity of temperature (in m year^{-1}) since the last glacial maximum (21,000 years BP). Current climate is a well-known determinant of plant richness at macro-scales on both islands and mainlands (Kreft & Jetz 2007; Kreft *et al.* 2008). Instead, Late

Table II.3.1. Minimum adequate models from ordinary least-square regressions for 23 oceanic archipelagos worldwide. Plant diversity components and their ratios were used as response variables and environmental variables as explanatory variables. Explanatory variables were grouped into biogeographic (*BioGeo*), climatic (*Clim*), and intra-archipelagic (*IntraArch*) variables. Model selection was based on values of the Akaike Information Criterion corrected for small sampling sizes (AICc) across models with all possible factor combinations. Coefficients were standardized; se = standard error; significance: **.** 0.1>*P*>0.05; * 0.05>*P*>0.01; ** 0.01>*P*>0.001; ****P*<0.001.

Response variable (R^2)	Explanatory variable	Category	Coefficient ± se	*t-value*	*P-value*
γ (R^2=0.88)	Intercept		2.48 ± 0.04	57.32	***
	Surrounding landmass proportion	*BioGeo*	0.21 ± 0.06	3.42	**
	Age	*BioGeo*	0.14 ± 0.05	2.70	*
	Annual mean temperature	*Clim*	0.18 ± 0.06	3.10	**
	Annual temperature range	*Clim*	0.18 ± 0.07	2.52	*
	Climate change velocity	*Clim*	−0.21 ± 0.05	−3.98	***
	Number of islands	*IntraArch*	0.15 ± 0.05	2.74	*
α (R^2=0.86)	Intercept		2.15 ± 0.04	57.43	***
	Surrounding landmass proportion	*BioGeo*	0.26 ± 0.05	5.23	***
	Age	*BioGeo*	0.11 ± 0.04	2.60	*
	Annual mean temperature	*Clim*	0.16 ± 0.05	3.27	**
	Annual temperature range	*Clim*	0.11 ± 0.06	1.88	.
	Climate change velocity	*Clim*	−0.20 ± 0.04	−4.54	***
β_A (R^2=0.82)	Intercept		2.15 ± 0.07	32.05	***
	Age	*BioGeo*	0.19 ± 0.08	2.58	*
	Maximum elevation	*BioGeo*	0.21 ± 0.09	2.42	*
	Annual mean temperature	*Clim*	0.44 ± 0.09	4.87	***
	Annual temperature range	*Clim*	0.38 ± 0.09	4.53	***
	Number of islands	*IntraArch*	0.21 ± 0.08	2.52	*
β_{nst} (R^2=0.75)	Intercept		1.93 ± 0.08	25.62	***
	Age	*BioGeo*	0.17 ± 0.08	2.15	*
	Annual mean temperature	*Clim*	0.38 ± 0.10	4.02	***
	Annual temperature range	*Clim*	0.30 ± 0.10	2.95	**
	Island area range	*IntraArch*	0.33 ± 0.09	3.78	***
β_{rpl} (R^2=0.85)	Intercept		1.70 ± 0.06	27.13	***
	Total land area	*BioGeo*	−0.37 ± 0.17	−2.18	*
	Surrounding landmass proportion	*BioGeo*	0.51 ± 0.11	4.72	***
	Climate change velocity	*Clim*	−0.43 ± 0.12	−3.71	**
	Number of islands	*IntraArch*	0.56 ± 0.12	4.59	***
	Mean distance between islands	*IntraArch*	0.17 ± 0.08	2.11	*
β_A/α (R^2=0.85)	Intercept		1.43 ± 0.17	12.35	***
	Total land area	*BioGeo*	3.45 ± 1.05	3.30	**
	Number of islands	*IntraArch*	1.40 ± 0.24	5.95	***
	Archipelago hull	*IntraArch*	−4.39 ± 1.05	−4.20	***
	Connectivity	*IntraArch*	−3.10 ± 0.96	−3.24	**
	Mean inter-island distance	*IntraArch*	1.11 ± 0.28	3.98	***
β_{rpl}/β_{nst} (R^2=0.79)	Intercept		0.78 ± 0.08	9.56	***
	Total land area	*BioGeo*	4.42 ± 1.32	3.35	**
	Island area range	*IntraArch*	−1.90 ± 0.36	−5.23	***
	Archipelago hull	*IntraArch*	−2.67 ± 0.94	−2.85	*
	Connectivity	*IntraArch*	−2.31 ± 0.98	−2.35	*
	Mean inter-island distance	*IntraArch*	0.45 ± 0.21	2.13	*

Quaternary climate change velocity reflects climate displacement rate as an important determinant of endemic species and can be interpreted as the required speed to keep track with climate change since the last glacial maximum while accounting for topography (Sandel *et al.* 2011). Mean values for all climatic variables were calculated for each archipelago based on values for individual islands taken from Weigelt *et al.* (2013a).

The six intra-archipelagic variables were range in island area (in km^2), environmental volume (unitless), number of islands (count), archipelago hull (in km^2), connectivity (unitless), and mean inter-island distance (in km). Island area range was calculated as the difference between minimum and maximum area size of islands within each archipelago. We calculated an environmental volume as integrative measure of intra-archipelagic environmental heterogeneity. We quantified the volumes occupied by the islands of each archipelago in the ordination space of a principal component analysis (PCA, axes 1–3, 72.4% of total variation) which included 17,883 islands worldwide and ten bioclimatic and physical variables (see Weigelt *et al.* (2013a) and Fig. V.3.1 for details). In contrast to maximum elevation as a measure of archipelagic environmental heterogeneity, this metric considers multiple factors contributing to heterogeneity among individual islands of an archipelago. To quantify the area of the entire archipelago, we calculated minimum convex hulls (in ArcGIS version 10) enclosing all islands of each archipelago and derived their areas at an equal area map projection. This represented the whole area occupied by an archipelago, including both land and ocean areas. We further calculated inter-island connectivity by integrating area sizes, inter-island distances, and spatial arrangement (introduced as 'integrated index of connectivity' by Pascual-Hortal & Saura 2006). Mean inter-island distance was calculated by averaging all pairwise shortest distances between island coastlines using an azimuthal equidistant map projection centred separately for each island (ArcGIS version 9.3.1.). All calculations were based on high-resolution island polygons (gadm version 1, Hijmans *et al.* 2009).

The values of biogeographic, climatic, and intra-archipelagic variables are provided in Tables V.3.3 to V.3.5. These tables also include additional variables used for initial single-predictor analyses, which were later excluded from multi-predictor analyses to avoid overfitting and multicollinearity (see Tables V.3.6 & V.3.7 for correlation matrices). To improve residual normality, we $\log_{10}$-transformed all diversity components and abiotic factors, except for archipelago age, annual mean temperature, and annual precipitation.

Statistical analyses

We applied multiple linear regressions and multi-model inference based on the Akaike Information Criterion corrected for small sampling sizes (AICc, Burnham & Anderson 2002) to assess the relative importance of each predictor variable across all possible variable combinations. To investigate whether relationships between abiotic variables and γ diversity are direct or indirect, we used structural equation models (SEMs) which allow evaluating hypothesized causal effects in datasets with multiple, hierarchically structured dependent variables (Grace *et al.* 2012).

As response variables in multiple regressions, we used the diversity components (γ, α, β_A, β_{rpl}, β_{nst}) and their ratios (β_A/α and β_{rpl}/β_{nst}). We calculated models for all possible combinations of the 15 predictor variables and used AIC_c to identify minimum adequate models for each response variable. Variable importance was assessed by weighting standardized regression coefficients by AIC_c-weights and adding them up for all models in which a variable was included (Burnham & Anderson 2002). Predictor variables were standardized (zero mean, unit variance) to obtain quantitatively comparable regression coefficients. To test for spatial autocorrelation in the residuals of minimum adequate models, we calculated global Moran's I values and compared non-spatial regression models with simultaneous autoregressive (SAR) models of the error type I (Kissling & Carl 2008). The optimal number of neighbours (tested for k = 1–15 neighbours) for building neighbourhood matrices were identified based on Moran's I values and their significance levels (Kissling & Carl 2008). Moran's I values for all model residuals were not significant ($P < 0.05$). We therefore present only results from non-spatial regression models below.

To prevent overfitting and problems arising from multicollinearity among predictor variables (see Tables V.3.6 to V.3.7), we reduced the number of predictors in SEMs by performing separate PCAs for the three groups of variables (*BioGeo*, *Clim*, and *IntraArch*). From each PCA, we considered all axes that cumulatively contained ≥ 75% of the variation. This resulted in two axes for the biogeographic PCA (*BioGeo 1–2*), three axes for the climatic PCA (*Clim 1–3*), and two axes for the intra-archipelagic PCA (*IntraArch 1–2*). We initially constructed full SEMs with all possible paths from the PCA axes to γ diversity and to the components of γ diversity, and from the components to γ diversity (Fig. V.3.2). We performed four SEMs to test the indirect influences of biogeographic, climatic, and intra-archipelagic variables on γ diversity via: i) α and β_A; ii) β_{rpl} and β_{nst}; iii) the ratio β_A/α; and iv) the ratio β_{rpl}/β_{nst} (Fig. V.3.2). From the full SEMs, we subsequently excluded non-significant paths with the highest P-values in a stepwise procedure until all remaining paths were statistically significant ($P < 0.05$). At each step, we evaluated residual correlations, modification indices, and model fits of the SEMs and used chi-square tests, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) as measures of model fit (Grace *et al.* 2012). All final SEMs had satisfactory fits as indicated by P-values of chi-square tests > 0.05, lower 90% confidence intervals of RMSEA < 0.05, and CFIs > 0.90 (Table V.3.8). We tested for spatial autocorrelation in SEMs by calculating Moran's I values for the residuals of multiple non-spatial ordinary least square regression models (OLS) similar to those in the final SEMs. In only two out of ten cases, Moran's I values (≤ 0.2) were statistically significant indicating spatial autocorrelation. For these models, we fitted SAR models of the error-type I (Kissling & Carl 2008) with similar neighbourhood structures as above. Model coefficients of spatial models only minimally diverged from the coefficients of OLS models (see Table V.3.5) and we thus report only non-

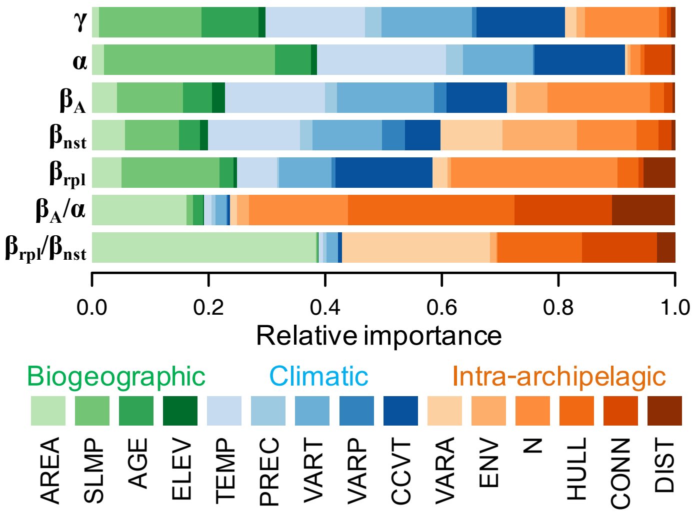

Figure II.3.2. Relative importance of abiotic variables affecting vascular plant diversity components and their ratios on 23 oceanic archipelagos worldwide. Relative importance was obtained from weighted standardized regression coefficients of linear regression models including all possible factor combinations on the basis of Akaike's Information Criterion corrected for small sampling sizes (AICc, see main text for details). Factors were grouped into three categories: biogeographic (green), climatic (blue) and intra-archipelagic (orange-brown). Note the high importance of biogeographic variables to α, γ, and β_{rpl}/β_{nst}, and the importance of intra-archipelagic variables for the β components and ratios. Variable abbreviations are: *AREA* - island area; *SLMP* - surrounding landmass proportion; *AGE* - age of the oldest island; *ELEV* - maximum island elevation; *TEMP* - annual mean temperature; *PREC* - annual precipitation; *VART* - variation in annual temperature (range); *VARP* - coefficient of variation of precipitation; *CCVT* - climate change velocity of temperature; *VARA* - variation in island area (range); *ENV* - environmental volume; *N* - number of islands; *HULL* - archipelago hull; *CONN* - connectivity; *DIST* - mean inter-island distance.

spatial SEMs below. Overall, spatial autocorrelation, and thus potential pseudo-replication in space, did not seem to play an important role in our dataset, probably because archipelagos are far from each other and their floras most likely originated from independent biogeographical dynamics.

All statistical analyses were performed in R statistical programming language (version 2.15.3, www.R-project.org). SEMs were calculated using library 'lavaan', Moran's *I* and SAR models were calculated using library 'spdep', and three-dimensional convex hulls for environmental volume were calculated using library 'geometry'.

Results

Both the absolute and relative contributions of the different diversity components varied greatly among the 23 archipelago floras (Fig. II.3.1). Gamma richness ranged between 27 and 1,379 species (mean = 489 ± 418 SD). The relative contributions of the α and β_A components to γ also varied considerably, with α contributing up to 94% on the Prince Edward Islands but only 15%

on the Kuriles (Fig. II.3.1). The β_{rpl} component had the highest contribution on the Juan Fernandez Islands (77% of β_A). Perfectly nested species assemblages were found on the Prince Edward Islands (β_{nst} 100% of β_A; Fig. II.3.1).

Biogeographic variables (surrounding landmass proportion and age) as well as climatic (annual mean temperature, temperature seasonality, and Late Quaternary climate change velocity) were the most important determinants of γ richness and the only significant determinants of α (Table II.3.1; for partial residual plots see Fig. V.3.3). All these variables, except for Late Quaternary climate change velocity, had positive effects on α and γ. Additionally, the number of islands also positively influenced γ (Table II.3.1). Biogeographic, climatic, and intra-archipelagic variables also affected the β components, showing mostly positive relationships (β_A, β_{nst} and β_{rpl}, Table II.3.1). Intra-archipelagic variables and total land area best explained the variation in β_A/α and β_{rpl}/β_{nst} ratios. An increase in total area, number of islands, mean inter-island distance, and a decrease in archipelago hull and connectivity significantly increased the β_A/α ratio (Table II.3.1). For the β_{rpl}/β_{nst} ratio, the range of island area rather than the number of islands was retained as significant determinant, decreasing the contribution of β_{rpl} (Table II.3.1).

Relative variable importance was given by AIC_c-weighted standardized regression coefficients of all possible regression models and revealed that the main determinants were generally consistent with the minimum adequate models, but with some noteworthy differences (compare Fig. II.3.2 and Table II.3.1). First, climatic variables were the strongest determinants of α, β_A and γ, but precipitation-related variables consistently played minor roles (Fig. II.3.2). Second, intra-archipelagic variables were the strongest determinants of β_{rpl}, β_{nst}, β_A/α and β_{rpl}/β_{nst}. Third, for β_A and β_{rpl}, the number of islands was the strongest intra-archipelagic determinant. Finally, the range of island areas and environmental volume also played an important role for β_{nst}.

SEMs revealed that both α and β components had strong direct effects on γ (compare path coefficients in Fig. II.3.3a and relative contributions in Fig. II.3.1). These effects were predominantly mediated via direct effects of biogeographic, climatic, and intra-archipelagic variables on α and β_A, respectively. In contrast, direct effects of biogeographic and climatic drivers on γ were considerably weaker than those on α and β_A, whereas intra-archipelagic variables did not show any direct effects on γ (Fig. II.3.3a). Both β_{rpl} and β_{nst} were explained by similarly strong direct effects of biogeographic, climatic, and intra-archipelagic variables whereas direct effects of these variables on γ were much weaker (Fig. II.3.3b). The β_A/α ratio was only affected by a strong negative effect of *IntraArch 1* (Fig. II.3.3c). No direct effect of intra-archipelagic variables on γ remained in this SEM, with γ being solely driven by biogeographic and climatic variables and by a positive direct effect of β_A/α (Fig. II.3.3c). For the β_{rpl}/β_{nst} ratio, only biogeographic and intra-archipelagic variables were important, whereas biogeographic and climatic variables directly influenced γ (Fig. II.3.3d). The β_{rpl}/β_{nst} ratio did not showed a statistically significant link to γ in this SEM (Fig. II.3.3d). In general, the effects of *BioGeo* and *IntraArch* axes were positive (except for β_{rpl}/β_{nst}) and those of *Clim* axes negative (compare Fig. II.3.3a–d with Fig. II.3.3e).

Discussion

Our study presents the most comprehensive analysis of plant diversity on archipelagos worldwide to date. Using archipelagos rather than islands as focal spatial units allowed us to analyze novel spatial (i.e. intra-archipelagic) variables along with classic biogeographic and climatic determinants of species diversity. This analysis revealed a strong effect of the internal spatial structure of archipelagos (e.g. mean inter-island distance and area range) on β components and showed that intra-archipelagic variables mostly have indirect effects on γ via β_A. In contrast, classical biogeographic and climatic variables predominantly affected γ diversity via effects on α. We synthesize these findings in a general framework for testing the effects of biogeographic, climatic and intra-archipelagic drivers on multiple components of species diversity (Fig. II.3.4). This conceptual framework provides relevant and testable predictions for other taxa and other archipelago-like systems.

Effects on the α component (H1)

Alpha was mostly influenced by biogeographic variables and by past and present-day climate (Table II.3.1, Figs. II.3.2 & II.3.3a), suggesting that intra-archipelagic spatial structure generally plays a minor role for α diversity within archipelagos (Fig. II.3.4). This supported H1 and can be expected because the additive α component is very similar to the number of species per island of most previous studies. For example, the importance of contemporary climate is in agreement with other island and mainland studies (Kreft & Jetz 2007; Kreft *et al.* 2008). The positive effect of temperature follows the global pattern of increasing species diversity towards the equator (Hillebrand 2004; Gillooly & Allen 2007) and might reflect the larger species pools of potential colonizers for tropical islands as well as positive effects on island carrying capacity. However, the unexpected positive effect of temperature seasonality might be caused by an overrepresentation of species-rich archipelagos in the subtropics of the Northern hemisphere and by the underrepresentation of species-rich tropical archipelagos in our dataset (due to insufficient data). Besides current climate, we also found negative effects of Late Quaternary climate change velocity on α (Fig. II.3.2). This driver has not yet been considered widely in island biogeography, but revealed a detectable influence of climate change since the last glacial maximum on current island diversity (in contrast to results for island palms, compare Kissling *et al.* 2012a).

Among the biogeographic determinants, α was positively correlated with island age and surrounding landmass proportion. The latter is in agreement with classic island biogeographic theory which predicts higher species richness on less isolated islands (MacArthur & Wilson 1963). However, the relationship between archipelago age and richness has not yet been investigated in island biogeography. So far, island biogeographic models have focused on the age of single islands (Whittaker *et al.* 2008) rather than on the archipelago age, which might entail complex temporal and spatial dynamics.

Effects on β components (H2)

Confirming H2, the β_A component was largely determined by the intra-archipelagic spatial structure of islands (Table II.3.1, Figs. II.3.2 & II.3.3a), suggesting that this group of variables is the key driver of beta diversity in archipelago-like systems (Fig. II.3.4). This became particularly evident for the β_A/α ratio, which expresses the relative importance of β_A over α independently from γ (Fig. II.3.3c). Increasing environmental heterogeneity (via environmental volume and island area range) and dispersal limitation (via higher mean inter-island distance and lower connectivity) positively affected species turnover, similar to observations from mainland systems (Leibold *et al.* 2004; Kraft *et al.* 2011; Stegen *et al.* 2013).

Both β_{nst} and β_{rpl} (Fig. II.3.3b) as well as the β_{rpl}/β_{nst}-ratio (Fig. II.3.3d) were also most strongly affected by intra-archipelagic variables, but the role of each specific intra-archipelagic variable varied between the components, supporting H2 (Table II.3.1, Figs. II.3.2 & II.3.3b & d). Nestedness was mainly determined by the range in island areas and factors that were also associated with α (temperature, temperature seasonality, and age). These effects could be explained by a larger area range with the smallest islands being able to sustain only subsets of species of larger islands (Patterson & Atmar 1986). Moreover, the smallest islands might only be able to have a nested subset of species of larger islands because they are too small for *in situ* speciation (Kisel & Barraclough 2010). In contrast, β_{rpl} was more strongly driven by the number of islands and the mean inter-island distance. Increasing number of islands and inter-island distance might facilitate species replacement by making new habitat available while limiting intra-archipelago dispersal and gene flow (Mouquet & Loreau 2003; Shaw *et al.* 2010) and by promoting speciation (Chiarucci *et al.* 2010).

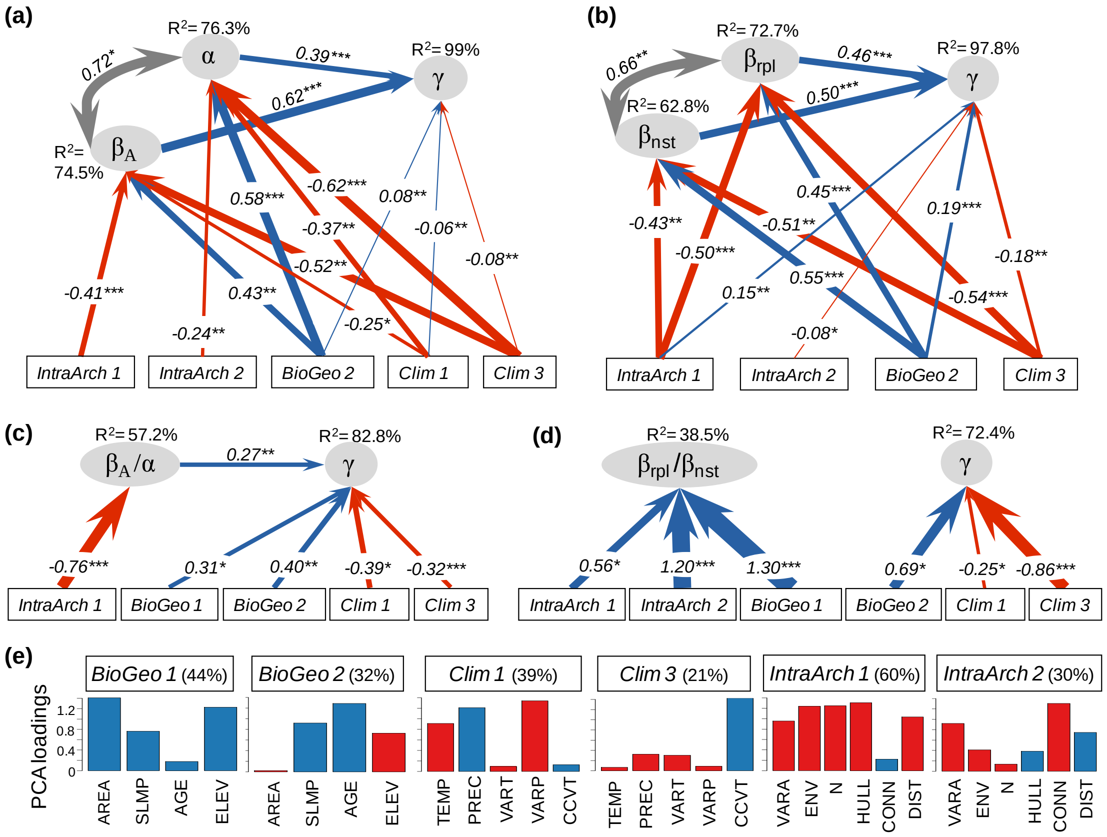

Figure II.3.3. Direct and indirect effects of biogeographic, climatic, and intra-archipelagic spatial factors on γ richness of vascular plants on 23 oceanic archipelagos worldwide. Structural equation models are based on principal component analysis (PCA) axes for (a) α and β_A influencing γ; (b) ratio β_A/α influencing γ; (c) β_A replacement (β_{rpl}) and β_A nestedness (β_{nst}) influencing γ; and (d) ratio β_{rpl}/β_{nst} influencing γ. Panel (e) illustrates PCA axes and the individual contributions of single variables to their main axes. PCA axes refer to biogeographic (*BioGeo 1–2*), climatic (*Clim 1* and *3*), and intra-archipelagic (*IntraArch 1–2*) variables, with the amount of variation explained by the axes given in parentheses (see legend of Fig. II.3.2 for abbreviations). Note that *Clim 2* was not significant for any diversity component. Blue colors illustrate positive and red colors negative relationships. Explained variance (R^2) is given on top of the response variables (grey circles). Standardized coefficients are given for each path. *P* values: * 0.05>*P*>0.01, ** 0.01>*P*>0.001, and ****P*<0.001. Arrow width is proportional to the effect size given by the coefficient. Note that to assess the actual relationship between specific abiotic variables and the response variables, it is necessary to consider the signal of the SEM path and the loading of the respective PCA axis.

Beta components were further considerably affected by present and past climate, surrounding landmass, elevation, age, and total land area (Table II.3.1, Figs. II.3.2 & II.3.3). These effects support the notion that higher heterogeneity (via elevation and land area), temperature, isolation and age are closely associated with rates of speciation and species turnover (Brown *et al.* 2004; Whittaker *et al.* 2008; Chiarucci *et al.* 2010). In fact, increasing isolation between islands within an archipelago hampers gene flow between populations and thus promotes opportunities for speciation and diversification (Rosindell & Phillimore 2011). However, effects of paleoclimatic changes on β components have rarely been addressed before, and this deserves further attention in biogeography.

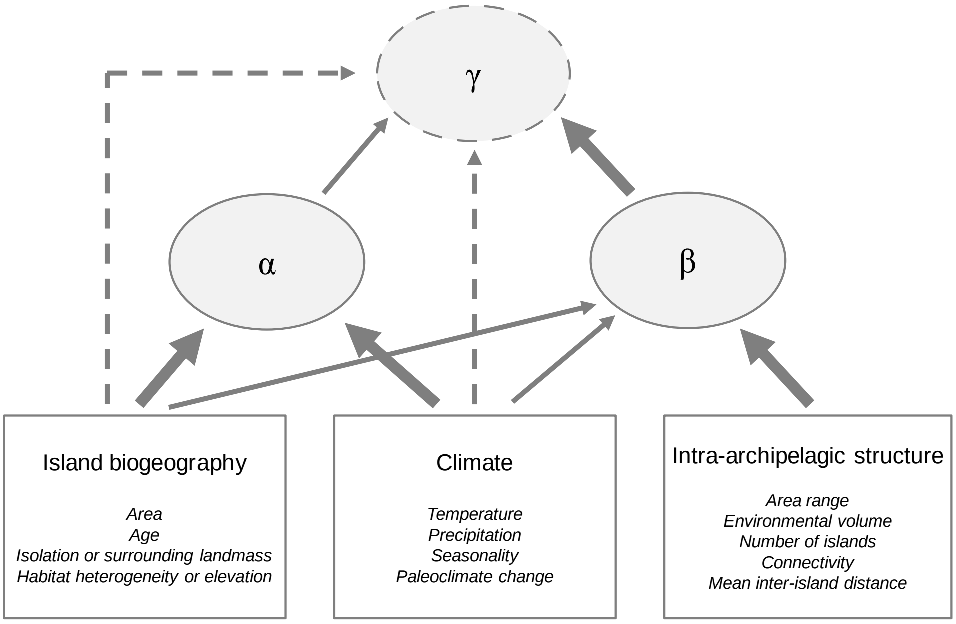

Figure II.3.4. A generalized conceptual framework for testing biogeographic, climatic and intra-archipelagic spatial effects on multiple components of species diversity (α, β, and γ) in archipelago-like systems. The strength of hypothesized relationships between variables is indicated with dashed arrows (weak effects), thin arrows (intermediate effects), and thick arrows (strong effects). The framework is derived from empirical results for vascular plant richness on oceanic archipelagos (this study), but could be tested more widely in any other archipelago-like system (e.g. alpine communities, coral reefs, freshwater lakes, isolated seamounts, isolated deserts, etc.).

Effects on γ diversity (H3)

Gamma diversity was predominantly driven by the direct effects of α, β_A, β_{rpl}, and β_{nst} (Fig. II.3.3a–b), supporting the hypothesized indirect effects of abiotic factors on γ (H3). Importantly, β had much stronger effects (std. path coefficient = 0.62) on γ than α (std. path coefficient = 0.39, Fig. II.3.3a). In fact, the relative importance of β_A over α (β_A/α) retained a positive direct effect on γ (Fig. II.3.3c). Hence, the intra-archipelagic variables which strongly affected β_A suggest a strong indirect effect of spatial variables on γ (Fig. II.3.4).

The strong direct effects of diversity components on γ were expected due to the additive diversity partitioning approach (compare Anderson *et al.* 2011). Yet, indirect effects were especially pronounced for intra-archipelagic spatial variables, which had no direct effect on γ when considering β_A/α and β_{rpl}/β_{nst} ratios (Fig. II.3.3c–d). Direct effects of abiotic factors on γ were observed for both biogeographic and climatic variables, albeit with weak effects (Table II.3.1, Fig. II.3.3c–d). The significant direct effects of age and surrounding landmass may reflect an interplay between geological history, speciation processes (including adaptive radiations), and island-hopping (Ricklefs & Bermingham 2002; Whittaker & Fernández-Palacios 2007; Losos & Ricklefs 2010; Rosindell & Phillimore 2011). Older archipelagos may have higher richness simply because they had more time for colonization and speciation. A negative effect of Late Quaternary climate change velocity on patterns of endemism has been reported for mainland faunas (Sandel *et al.* 2011). Here, we showed a global-scale imprint of paleoclimatic change on α and β components, and thus an effect that acts indirectly on γ richness of archipelagic systems. In contrast to common assertions that geological dynamics are the main factor for determining species richness of archipelagos (Losos & Ricklefs 2010), we suggest that paleoclimatic fluctuations might be equally important.

The key role of β as a driver of γ, evident from the direct positive effect of β_A/α on γ (Fig. II.3.3c), has also been recently reported for birds in mainland systems (Stegen *et al.* 2013). Such a relationship could be caused by dispersal limitation, niche specialization or competitive exclusion (Veech & Crist 2007; Stegen *et al.* 2013). Moreover, adaptive radiations, taxon cycle dynamics and island-hopping (Gillespie & Roderick 2002; Losos & Ricklefs 2009; Kisel & Barraclough 2010) are also important for species turnover (Chiarucci *et al.* 2010), and our results suggest that they indirectly affect archipelagic γ diversity.

Conclusions

A promising approach to analyze diversity patterns in archipelago-like systems is to partition overall species diversity into different α and β components and to test potential hypotheses about underlying processes in a common framework (Fig. II.3.4). Our results from oceanic archipelagos indicate that γ is predominantly determined by indirect effects of abiotic factors via its α and β components, with β being more important for archipelagic γ diversity than α. To understand archipelagic species diversity, it is therefore key to consider β, its components, and their possible drivers. We show that β and its components on oceanic archipelagos are mostly affected by intra-archipelagic spatial variables whereas α is most strongly related to climate and island biogeographic drivers. Hence, the consideration of such spatial factors is essential for assessing diversity components on island-like systems. Our framework derived here from empirical results for vascular plant diversity on oceanic archipelagos (Fig. II.3.4) can be tested more widely for other taxa (e.g. microbes, insects, vertebrates) or other archipelago-like systems (e.g. alpine habitats, isolated deserts, freshwater lakes, coral reefs, isolated seamounts).

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Chapter II.4

Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern of fern diversity in the Southeast Asian archipelago

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Abstract

Aim To investigate if the equilibrium theory of island biogeography (ETIB) is equally applicable at regional and local spatial scales and if the 'echo pattern', the correlation between regional species pool and local diversity, by which the diversity of the regional species pool "trickles down" to local scales, influences local diversity equally across a range of sampling scales.

Location Twelve mountain regions on islands of varying size, degree of isolation and environmental conditions in Indonesia and the Philippines.

Methods We sampled ferns in standardized field plots within a fixed spatial design at six different spatial scales (grain size varied from plot to island). Using ordinary least squares regression and relative variable importance, we tested for the predictive power of area and isolation as well as local and regional environmental factors for explaining diversity at the different spatial scales.

Results Consistent with MacArthur and Wilson's ETIB, we found strongest correlations of area and isolation at regional scales. The explanatory power of area increased with increasing spatial scale. The slope of the negative relationships among diversity and isolation decreased with increasing spatial scale. We found evidence for an 'echo pattern' at large to intermediate but not at small spatial scales.

Main conclusions Area and isolation are strong predictors of biodiversity at regional scales. The size of the species pool has a scale-dependent influence on diversity at smaller scales but is unimportant at the most local scale where environmental conditions prevail as predictors of diversity. To make predictions about local diversity on islands it is therefore important to take the scale-dependence of the 'echo pattern' into account.

Introduction

Island systems have long played a crucial role in biogeographical and biodiversity research because they provide comparatively simple systems with clearly defined subunits of usually varying sizes and ecological conditions (Whittaker & Fernández-Palacios 1998). The classical equilibrium theory of island biogeography (ETIB) predicts that the number of species that occur on an island is mainly dependent on the balance between species immigration and extinction as determined by species number as well as the surface area of the island and its isolation (MacArthur & Wilson 1967), although current models also integrate island age and geological processes (Whittaker *et al.* 2008).

According to the ETIB, species diversity on islands is positively related to island area and negatively to isolation. Area is the most fundamental parameter influencing diversity patterns on islands (Arrhenius 1921; Connor & McCoy 1979; Lomolino 2001; Kreft *et al.* 2008) and can have various effects on species diversity at different spatial levels (Rosenzweig & Ziv 1999; Whittaker *et al.* 2001). A direct effect at the regional scale applies to the number of species that can coexist within a given region (MacArthur & Wilson 1967). It is still unclear, however, to which degree the increase of species numbers on larger islands is determined by the increase of area *per se* or by the larger number of habitats (Triantis *et al.* 2003; Kallimanis *et al.* 2008) influencing both the maximum number of co-occurring species and the rate of speciation (Losos & Schluter 2000; Kisel & Barraclough 2010). In contrast to area, isolation shows inverse relationships with the probability of dispersal to an island and the chance of its colonization. Continuously arriving propagules increase population viabilities of species present on less isolated islands ('rescue effect', Brown & Kodric-Brown 1977). On large islands, the effect of isolation may decrease since large islands receive more immigrants ('target area effect', Whittaker & Fernández-Palacios 1998) and serve as better arenas for *in situ* speciation (Losos & Schluter 2000; Kisel & Barraclough 2010). Finally, gene flow to island populations is negatively related to isolation, resulting in a higher chance of speciation on remote islands (Heaney 2000).

Species diversity is also known to be dependent on spatial scale, with different processes acting at different scales (Levin 1992; Whittaker 2000; Whittaker *et al.* 2001; Triantis *et al.* 2012). Therefore, variables explaining species diversity at a local spatial scale may not be the same as those accounting for diversity at regional spatial scales (Willis & Whittaker 2002; Triantis *et al.* 2012). While at large scales evolutionary history and energy availability are important factors, at small scales dispersal limitation or random processes might prevail (Triantis *et al.* 2012). This scale dependence also applies to the effects of area and isolation (Karger *et al.* 2011; Gillespie *et al.* 2013; Weigelt & Kreft 2013).

Aside from the above mentioned effect of area at the regional scale, at the local scale, larger sampling areas typically include more species because they more completely sample the regional species pool (Connor & McCoy 1979). However, even if sampling area is held constant, regional area will influence local species indirectly via its effects on the regional species pool ('echo pattern' sensu Rosenzweig & Ziv 1999). Local communities can be perceived as dynamic samples from the regional species pool (Terborgh 1973; Graves & Gotelli

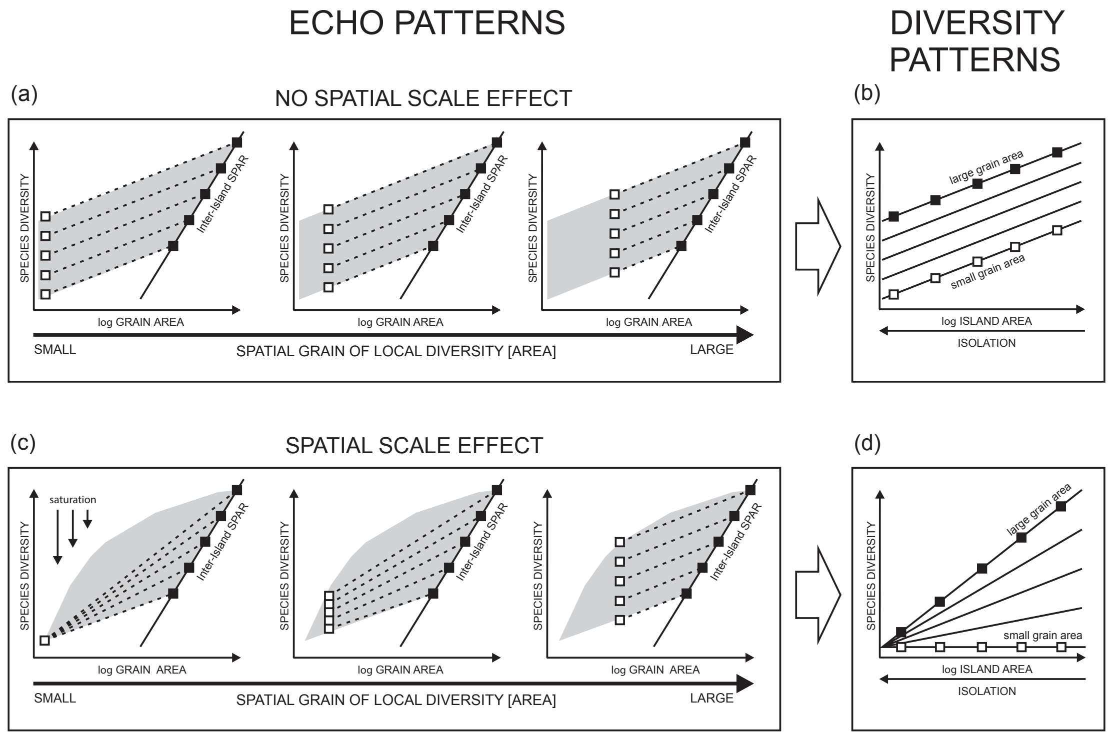

Figure II.4.1. Schematic representation of how the grain size at which local diversity is assessed changes the way regional diversity (black squares, solid line) translates into local diversity (white squares; modified after Rosenzweig & Ziv 1999). 'Echo patterns' (a, c) show the relation between regional diversity and local diversity within islands, diversity patterns (b, d) show the patterns of diversity at different grain sizes across islands. If grain size does not affect how regional diversity translates into local diversity (no spatial scale effect) intra-island species area relationship (SPARs; dashed lines) are parallel lines at all spatial scales (a). This results in parallel species area relationships when species diversity patterns assessed at different grain sizes are plotted over island area and isolation (b). If grain size affects intra-island SPARs (spatial scale effect; c), e.g. due to an increase in species saturation at smaller spatial scales, the resulting diversity patterns will show an increase in species diversity only for large grain sizes, but not for small grain sizes (d). The grey area shows the potential species diversity a local sampling site can harbour in relation to regional diversity.

1983; Cornell 1985; Ricklefs 1987) with the size of the surrounding area as a surrogate of the regional species pool (Terborgh & Faaborg 1980; Cornell & Lawton 1992; Caley & Schluter 1997; Cornell 1999; Romdal & Grytnes 2007).

The 'echo pattern' has potential impact on island biogeography theory across spatial scales since it shows how local diversity is affected by the regional diversity it emanates from. The ETIB predicts local diversity to continuously increase with an increase of the regional species pool (or regional diversity) due to higher immigration rates (MacArthur & Wilson 1967; Kelly *et al.* 1989). Therefore, independent of the spatial grain chosen to assess species diversity, higher regional diversity should always result in a higher local diversity (Fig. II.4.1a). Assuming this relationship between regional and local diversity, species diversity is expected to increase with island area and decrease with its isolation independent of the spatial grain at which species diversity on an island is assessed (Fig. II.4.1b). In contrast, if the spatial grain at which local diversity is assessed influences the way regional diversity translates into local diversity

(Fig. II.4.1c), no consistent relationship with island area and isolation is expected at the smallest spatial grain (Fig. II.4.1d). Clearly, a limited regional species pool limits the number of co-occurring species in a local community, but local diversity may not increase continuously with the size of the regional species pool since local communities may become saturated at some point and local diversity may remain constant even if regional diversity increases (Huston 1999; Srivastava 1999). Consequently, species diversity at small spatial grains would be more influenced by local environmental conditions limiting the number of individuals that are able to survive in a community rather than by immigration from the regional species pool.

Islands provide ideal testing grounds for investigating the ‘echo pattern’ and its scale-dependent influence on the ETIB, since their regional species pools can be defined using island area and island isolation, which are directly related to the number of potential species that can occur within a local sampling site on an island. While most mainland studies on local species diversity either share a common species pool or have species pools that overlap to unknown degrees (e.g. the Amazonian lowlands, Tuomisto *et al.* 2003). The species pool contains all those species that could, in theory, disperse to a local community within the study area. On islands, distinguishing the species pool is therefore possible by using the area of the island, harbouring the ‘island’ species pool, and isolation, representing the immigration from the ‘mainland’ species pool. However, while several studies have investigated drivers of species diversity focusing on the scale-dependence of species diversity (Crawley & Harral 2001; Lennon *et al.* 2001; Rahbek & Graves 2001) an investigation on how well the two main factors of the ETIB, area and isolation, predict species diversity at different scales has not yet been conducted. To tackle this, we selected twelve islands of different size and degree of isolation in Indonesia and the Philippines and sampled fern diversity at six spatial grains. We tested if regional area and isolation are strong predictors of diversity at all grain sizes or if environmental conditions are more important at a small grain size. We formulated two competing hypotheses in accordance with the above mentioned theoretical assumptions to address the question whether the ETIB is equally applicable from regional (island level) to local (plot level) scales.

H1: Regional area and isolation are strong predictors of species diversity at all grain sizes. The ‘echo pattern’ will lead to an equal increase in diversity with regional area at all grain sizes. Therefore, the ETIB is equally applicable at all spatial scales.

H2: Regional area and isolation are strong predictors of species diversity only at large grain sizes. The species pool affects local diversity depending on the grain size in which local diversity is assessed. The biogeographical effects of regional area and isolation resulting from immigration from the regional species pool are diluted at local scales where local environmental conditions set an upper limit to species diversity. Therefore, the ETIB is applicable only at regional spatial scales.

Methods

Study design

Study sites

We selected 12 mountain regions on islands of different size, degree of isolation and environmental conditions in Indonesia and the Philippines (Fig. II.4.2). On each island, sampling sites were located between 1,100 m and 1,200 m within the main mountain range of the island (Table II.4.1). We chose this elevational belt for two reasons: First, it has a high number of fern and lycophyte (henceforth called fern) species (Bhattarai *et al.* 2004; Carpenter 2005; Kluge *et al.* 2006; Kessler *et al.* 2011), enabling us to collect statistically relevant samples. Second, human footprint in this elevation is the lowest worldwide (Nogues-Bravo *et al.* 2008), providing us with mostly undisturbed natural ecosystems.

Ferns as a model group

Ferns are distributed worldwide, and are independent of biotic pollination and animal vectors because of their spore dispersal (Barrington 1993). The high species diversity of ferns allows statistical inference of the documented data, and the relatively low dependence from biotic vectors link patterns of distribution directly to abiotic factors.

Transect design

Samples were taken in standardized plots of 20 m x 20 m. This plot size has previously been used for surveys of local fern diversity (Kessler 2001; Kluge *et al.* 2006) and is large enough to be representative, but also small enough to be ecologically homogeneous and to allow rapid and efficient surveys (Kessler & Bach 1999). We used a fixed sampling design of transects of four plots with a distance of 20 m. In each mountain range, two such transects were established in pristine forests 100 m apart at 1,100 m and two at 1,200 m (Fig. II.4.2).

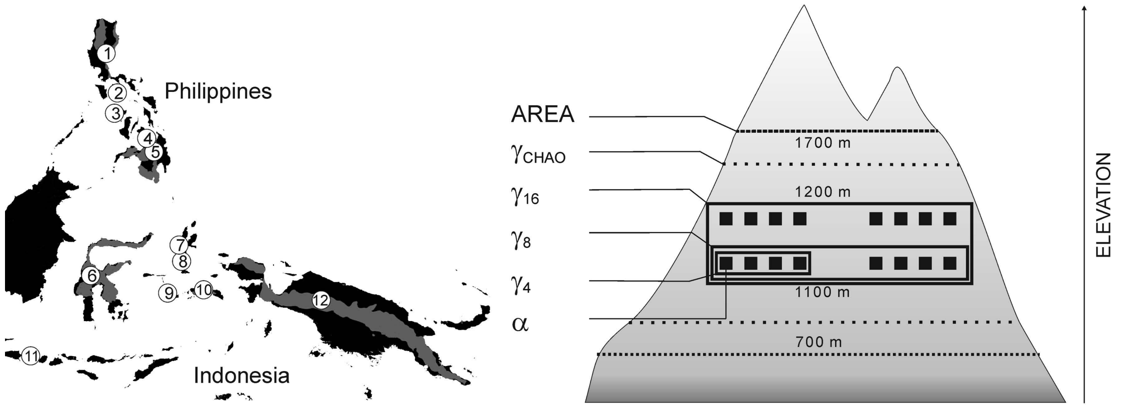

Figure II.4.2. Study locations and sampling design of fern diversity on Southeast Asian islands. Left: Sampling locations (white circles with numbers; Table II.4.1) spanning the gradients of habitat area and isolation in the Malesian Archipelago and New Guinea. Right: Schematic representation of the sampling design consisting of 16 plots of 20 x 20 m each (mean richness = α) with one transect consisting of four plots at fixed distances of 20 m (γ_4). Two transects of four plots each were arranged 100 m apart (γ_8), each at both 1100 m and 1200 m elevation (γ 16). γ_{CHAO} as an approximation of the local species pool was calculated using a species diversity estimator (Chao 2) across all 16 plots. Habitat area was measured as the land surface of each studied mountain range per island between 700 m and 1700 m a.s.l. (grey shades on islands, left), corresponding to the mean elevational range amplitude (1000 m) of montane fern species.

Plant sampling

For each plot, we assembled a list of all fern species. Epiphytic species were surveyed by a combination of climbing trees, cutting selected branches, looking for fallen branches on the ground, and by the use of binoculars. This approach has previously been successfully applied in studies of this kind (Kessler 2001; Kluge *et al.* 2006; Kessler *et al.* 2011). Every fern species in each study region (but not in each plot) was collected for later determination and deposited in the Herbarium Zurich (ZH), Herbarium of the Central Mindanao University (Central Mindanao University Herbarium), Herbarium Bogor (BO), and the Herbarium University of California, Berkley (UC).

Diversity and spatial scale

We defined α diversity as the mean diversity of all 16 20 m x 20 m plots. γ_4 diversity was defined as the total number of species found in all four plots per transect (calculated as the mean of four transects per site), γ_8 diversity as the total number of species found in two transects of a total of eight plots at a given elevation (calculated as the mean of two transects per site), and γ_{16} diversity as the total number of species found in four transects of a total of 16 plots. γ_{CHAO} diversity was calculated using the Chao 2 estimator (Chao 1984) based on γ_{16} diversity and the number of singleton and doubleton species recorded. γ_{reg} diversity was defined as the total number of fern species on an island quantified as the total number of species listed in the Flora Malesiana (Kalkman & Nooteboom 1998).

The term “scale” in this context refers to the size of the units used in the sampling of the assemblages or grain size (Whittaker *et al.* 2001; Scheiner 2011) and ranges from 400 m² (α) to the area of the island (γ_{reg}). We considered species numbers at the levels of α to γ_{CHAO} as estimates of local species diversity because they refer to fern assemblages at scales of <1 km^2, i.e. at a scale where direct species interactions are likely to occur. As regional diversity estimates, we used both γ_{reg} and γ_{CHAO}. The latter was included both in the local and regional scales because while γ_{CHAO} is a subset of γ_{reg} and hence “local” in this regard, at the same time it represents a narrower “regional” species pool from which the even more local species assemblages (α - γ_{16}) are recruited.

Explanatory variables

We used area, isolation, habitat heterogeneity, bioclimatic, and edaphic characteristics to explain species diversity at the different spatial scales.

Area

As area, we defined the total habitat area within a mountain range where the sampling sites were located. For ferns, which have their maximum diversity at mid elevations and few lowland species (Bhattarai *et al.* 2004), the lowlands are dispersal barriers for most species, rendering the mountain ranges the actual habitat islands. Using the whole surface area of an island would therefore be misleading. We calculated habitat area based on the total surface area of the elevational belt ranging from 700 m to 1,700 m. This corresponds to the elevational range amplitude of the majority of montane fern species (Bhattarai *et al.* 2004; Carpenter 2005; Kluge *et al.* 2006; Kessler *et al.* 2011) and allows an approximation of the area which hosts the species pool from which the local assemblages are recruited from. We used ArcGis 10 (ESRI, Redlands) to calculate the surface area of the respective mountain ranges based on SRTM topographic data at 90-m resolution (Jarvis *et al.* 2008).

Table II.4.1. Locations of the sampling sites of fern diversity in Indonesia and the Philippines. The number refers to the location of the island in Fig. II.4.2.

No.	Island	Mountain/Site	Latitude	Longitude	Habitat area/site [km²]	Island area [km²]
1	Luzon	Mingan Mountains	15°25'N	121°24'E	390	104688
2	Sibuyan	Mt. Guiting Guiting	12°26'N	122°33'E	50	445
3	Panay	Mt. Madia-as	11°21N	122°08'E	787	12011
4	Camiguin	Mt. Timpoong	09°11'N	124°42'E	29	238
5	Mindanao	Mt. Kitanglad	08°08'N	124°55'E	5854	97530
6	Sulawesi	Toro, Lore Lindu NP	01°29'S	120°03'E	30557	174600
7	Tidore	Gunung Kiematubu	00°40'N	127°24'E	11	116
8	Bacan	Gunung Sibela	00°42'S	127°31'E	110	1900
9	Buru	Wafehai	03°13'S	126°34'E	2022	8473
10	Seram	Manusela NP	02°59'S	129°11'E	1451	17100
11	Lombok	Gunung Rinjani	08°20'S	116°24'E	799	4725
12	New Guinea	Pass Valley	03°46'S	139°14'E	173416	780000

Isolation

Following Weigelt and Kreft (2013), we empirically chose a measure of island isolation comparing metrics that represent different isolation concepts and source landmasses (see Table V.4.1). Since the ETIB had been formulated for entire islands, we selected the isolation metric based on the model fit of γ_{reg} in dependence on area and isolation (γ_{reg} ~ area + isolation) considering only models that showed the expected negative relationship among isolation and species diversity. We used the Akaike Information Criterion (AIC, Burnham & Anderson 2002) as measure of model fit. The distance of a mountain range to the nearest mountain range of at least 100 km² on the mainland (Asia or Australia) received strongest support for as explanatory variable for fern species diversity and we thus chose this metric for further analyses. Metrics that considered the amount of mountain area in the surroundings of the mountain ranges did not show consistent relationships to diversity at any spatial scale (see Table V.4.1). Distances were measured at azimuthal equidistant map projections using the ‘near table’ tool in ArcGis 9.3.1 ESRI, Redlands). Mountain ranges were defined as areas above 700 m a.s.l. according to SRTM topographic data at 90-m resolution (Jarvis *et al.* 2008).

Environmental variables

We used global temperature and precipitation models of nineteen different climatic variables derived from WorldClim – Bioclim (Hijmans *et al.* 2005) at a resolution of 30 arc-seconds (Weigelt *et al.* 2013a). At the local scale ($\alpha - \gamma_{CHAO}$), bioclimatic data was extracted for the location of the sampling plots. At the regional scale (γ_{reg}, γ_{CHAO}), we extracted the bioclimatic variables as the mean over the whole mountain range in which the sampling site was located.

γ_{CHAO} has been included as both local and regional, since it has been calculated on the basis of local data, but represents a more regional diversity.

Relative air humidity is a crucial environmental factor for ferns because of their relatively poor evaporative control (Kluge *et al.* 2006; Kessler *et al.* 2011), but measuring it *in situ* over long periods of time requires considerable effort. Therefore, we used bryophyte cover on trees as proxy for relative air humidity which has been verified for five sites within the Philippines using data loggers for relative humidity (Karger *et al.* 2012). We also included local environmental factors such as mean inclination of the plot and canopy cover that were visually estimated in each plot. Soil samples were taken from every plot and analyzed for 15 different soil parameters (see Table V.4.2).

Because the factors potentially co-vary and the use of more explanatory variables than observed variables violates the conditions for regression analysis, we reduced the environmental variables for regional climatic conditions (temperature and precipitation), as well as local environmental conditions using Principal Components Analysis (PCA). PCA axes were selected using a threshold of 70% variance explained (see Table V.4.3). Where applicable, variables were zero mean unit variance standardized to account for different measuring units.

Diversity models

To test the applicability of the ETIB of MacArthur and Wilson (1967) at varying spatial scales, we compared the slopes of regional area and isolation as predictors of fern species diversity assessed at small grain size (α) to diversity assessed at larger grain size (γ scales). Additionally we used regional species diversity (γ_{reg}) as predictor of species diversity at smaller grain sizes. We used partial residuals to visualize the effect of each factor accounting for the respective co-variable in linear multi-predictor models ($S \sim A + I$), with S = species diversity at a given grain size, A = habitat area, I = island isolation.

To account for regional differences in bioclimate and microclimatic, edaphic and structural conditions at plot level, we extended the models about select axes derived from the bioclimate and plot-environment PCAs. The relative importance of each predictor in the multi-predictor framework was assessed using the *pmvd* metric in the R-package *relaimpo* (Grömping 2006). All statistical analyses were performed using R statistical software version 2.14.2 (R Development Core Team 2010).

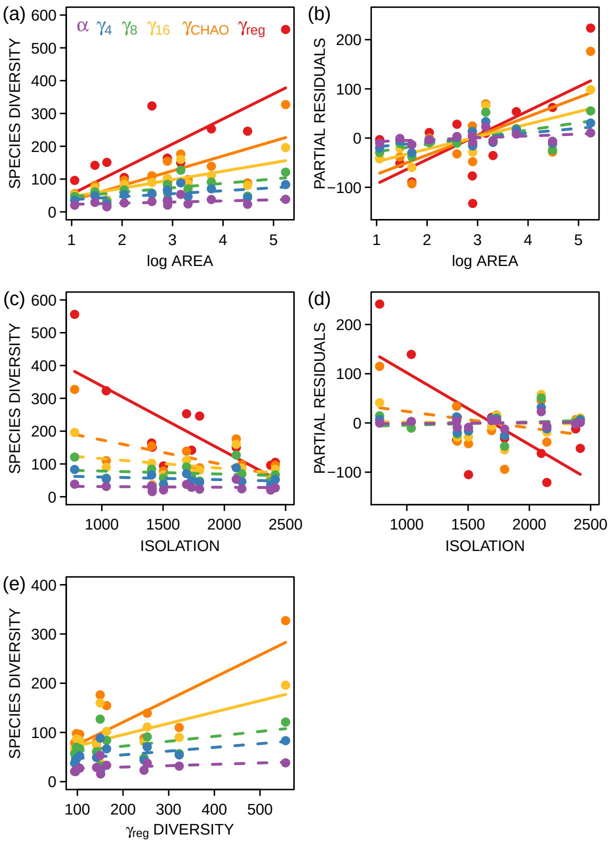

Figure II.4.3. Fern diversity on Southeast Asian islands across different spatial scales plotted over regional habitat area (a) and isolation (c) as well as partial residual plots accounting for the effect of the respective co-variable. Partial residuals are given for area (b) partitioning out the effect of isolation and (d) partitioning out the effect of area. (e) shows the relationship if γ_{reg} is used as explanatory variable instead of habitat area. Area was measured as the land surface of each studied mountain range per island between 700 m and 1700 m a.s.l. and isolation was quantified as the distance to the nearest mountain range at the mainland of Asia or Australia. Spatial grain sizes are colour-coded: α = violet, γ_4 = blue, γ_8 = green, γ_{16} = yellow, γ_{CHAO}= orange, γ_{reg}= red. Regression lines are drawn using ordinary least squares regression. Solid lines = significant ($P < 0.05$), dashed lines = not significant ($P > 0.05$).

Results

The ETIB of MacArthur and Wilson (1967) applied best at regional scales (Fig. II.4.3, Table II.4.2). Species-area slopes increased with spatial grain, but the relationships were significant only from the γ_{16} level upwards. These results were consistent both accounting for the effect of isolation in the multi-predictor models and disregarding it (Fig. II.4.3). The slopes of the negative relationships between diversity and isolation decreased with increasing spatial grain. However, this relationship was significant only at the island level (γ_{reg}). The explanatory power of the equilibrium model measured as R^2 increased monotonically with the spatial grain from 0.18 (α) to 0.74 (γ_{reg}; Table II.4.2). Similar patterns arose when species diversity at different grain sizes were plotted over γ_{reg} as an alternative explanatory factor for fern diversity at several smaller spatial grains (Fig. II.4.3e, Table II.4.2).

The relative importance of area decreased with the spatial grain of the units at which diversity was measured (Table II.4.3). Only when diversity was measured as the diversity of the entire island (γ_{reg}), relative importance of area was lower than expected from the linear decrease. The pattern of isolation as predictor of fern species diversity was less pronounced (Table II.4.3).

However, a decrease of relative importance from regional and Chao diversity to plot level diversities was apparent. Temperature did not explain diversity at any given grain size (Table II.4.3). Precipitation was only important at regional level but not at grains smaller than γ_{CHAO} (PRECPC2$_{\mathrm{reg}}$; Table II.4.3). Local environmental conditions (ENVPC3) showed a clear increase in relative importance with decreasing spatial grain (Table II.4.3). Consequently, maximum relative importance of environmental conditions was found at the α level (Table II.4.3).

Discussion

At the regional scale (γ_{reg}), we found the expected relationships of species diversity and both per mountain range area and isolation, as predicted by the classical theory of island biogeography (MacArthur & Wilson 1967; Whittaker & Fernández-Palacios 1998). In contrast, the marked decline in importance of area and isolation for diversity measured at smaller spatial scales shows that the ETIB loses its predictive power with decreasing spatial scale from regional to plot level (Fig. II.4.3, Table II.4.2).

At the smallest grain size (α) diversity was neither correlated with regional area nor with isolation. Based on these results, we have to reject our hypothesis that the ETIB is equally applicable across spatial scales (H1) in favour of a spatial scale effect on species diversity on islands (H2). This leads us to conclude that the influence of the species pool on local diversity is scale-dependent and decreases with decreasing spatial scale. A possible explanation for this pattern could be that local (α) diversity is saturated limiting the number of species which can migrate into local communities from the regional species pool and diversity becomes less saturated at larger scales (Fox & Srivastava 2006). A local community is considered saturated when the maximum number of species that can disperse into the community, find a suitable niche and keep a viable population size, is reached (Fox & Srivastava 2006). In addition, a community can be saturated simply because the upper limit of species diversity is reached due to ecological constraints (Srivastava 1999). The strong increase in the importance of environmental factors with decreasing spatial scale would favour the hypothesis of environmentally constrained saturation (Table II.4.3). At the α scale, species diversity thus can be considered to be saturated since the maximum fern diversity possible under the current environmental conditions appears to have been reached. An increase in the species pool can therefore have no effect on local species diversity, since the maximum number of species that the local assemblages can hold has already been reached.

Table II.4.2. Model statistics for regional area and isolation (left) and γ_{reg} (right) as descriptors of fern diversity at different spatial scales at mountain ranges on Southeast Asian islands (ordinary least squares regression). Area was measured as the land surface of each studied mountain range per island between 700 m and 1700 m a.s.l. Isolation was quantified as the distance to the nearest mountain range at the mainland of Asia or Australia. est. = estimated values. Significance: * ($p < 0.05$), ** ($p < 0.01$).

	Regional area and isolation							γ_{reg}				
	Intercept		**Area**		**Isolation**		**R^2**	**Intercept**		**γ_{reg}**		**R^2**
	est.	t	est.	t	est.	t		est.	t	est.	t	
γ_{reg}	303.63	2.39 *	49.38	2.37 *	-0.15	-2.88 *	0.74	-	-	-	-	-
γ_{CHAO}	64.21	0.70	39.05	2.59 *	-0.03	-0.91	0.57	29.68	0.63	1.40	4.20 **	0.64
γ_{16}	26.56	0.47	25.40	2.72 *	0.00	-0.13	0.52	-0.90	-0.01	2.10	3.05 *	0.48
γ_{8}	18.26	0.42	14.71	2.05	0.01	0.38	0.34	45.88	0.46	2.12	1.64	0.21
γ_{4}	24.24	0.83	9.39	1.95	0.00	0.15	0.33	3.04	0.03	3.59	1.94	0.27
α	15.32	0.89	3.80	1.35	0.00	0.28	0.17	56.68	0.47	4.79	1.25	0.13

Isolation did not show the same pronounced patterns as area across spatial scales. Although a decline in the importance of isolation was visible, this was only marginally significant. In fact, only two of the tested isolation metrics showed the expected significant negative effect, and only at the largest scale (γ_{reg}; see Table V.4.1). This might be partly due to the relatively small sampling size of twelve islands, but most likely reflects the fact that the variability of isolation among our study islands (3-fold) was much less than that of area (15,000-fold). Furthermore, isolation in a set of islands as complex as the Southeast Asian archipelago is difficult to quantify since inter-island connectivity might affect the degree of isolation of small islands more than that of large islands and a common source pool for all islands is hard to define. In addition, the comparatively low importance of isolation might also be linked to a high degree of speciation which may counteract the negative effect of isolation on species diversity, especially on large islands such as New Guinea or Mindanao (Kisel & Barraclough 2010; Weigelt & Kreft 2013).

Among the regional environmental variables, precipitation appeared to be important for fern diversity at regional and intermediate scales (γ_{reg}, γ_{CHAO}). The influence of precipitation on regional fern diversity has been shown before at a global scale for ferns (Kreft *et al.* 2010) and overall for vascular plants (Kreft & Jetz 2007). Its importance, however, declines towards smaller scales where local environmental factors become more important. In contrast, temperature did not show any relation to species diversity at any scale (Table II.4.3). This is not surprising considering that all of our investigated islands are within the tropics without a pronounced gradient in mean annual temperature and that water-related variables are more likely drivers of vascular plant diversity in high-energy regions (Kreft & Jetz 2007). However, data constraints of WorldClim might be problematic in this context as WorldClim is known to perform especially poorly in tropical mountain regions (Soria-Auza *et al.* 2010). We therefore caution against an ecological inference from these factors in this case.

Local environmental factors such as soil fertility and microclimatic conditions in contrast varied extensively at the grain size of one study site, and therefore showed a stronger correlation with

Table II.4.3. Relative variable importance of explanatory variables of fern diversity at different spatial scales in mountain ranges on SE Asian islands. Area = area of the mountain range between 700 m and 1700 m a.s.l., Isolation = distance to nearest mountain range at the mainland, TEMPPC1reg = regional temperature PCA axis 1, PRECPC1reg = regional precipitation PCA axis 1, PRECPC2reg = regional precipitation PCA axis 2, TEMPPC1 = local temperature PCA axis 1, PRECPC1 = local precipitation PCA axis1, ENVPC3 = local environmental conditions PCA axis 3. Relative importance was quantified using the pmvd metric (Grömping 2006) based on ordinary least squares regression models including all (significant) factors. ENVPC1 and ENVPC2 are not shown here due to lacking predictive power compared to ENVPC3.

	γ_{reg}	γ_{CHAO}	γ_{16}	γ_{8}	γ_{4}	α
Area	0.26	0.26	0.32	0.28	0.21	0.10
Isolation	0.38	0.10	0.07	0.04	0.04	0.03
TEMPPC1$_{reg}$	0.02	0.03	-	-	-	-
PRECPC1$_{reg}$	0.11	0.07	-	-	-	-
PRECPC2$_{reg}$	0.23	0.15	-	-	-	-
TEMPPC1	-	0.02	0.01	0.01	0.01	0.01
PRECPC1	-	0.02	0.01	0.04	0.05	0.07
ENVPC3	-	0.31	0.46	0.52	0.61	0.67

species diversity at the local scale compared to regional environmental variables. Local environmental factors are known to also increase regional diversity when more environmental conditions are encountered by using a larger number of sampling plots on large islands compared to small islands (Sfenthourakis & Panitsa 2012), contrary to the equal number of plots per island used in this study. We therefore caution to make the inference that local environmental factors do not matter for regional diversity. They can influence regional diversity, however, only when most of their within island variability is assessed to reflect regional variation of local environmental conditions (Sfenthourakis & Panitsa 2012).

By providing evidence for a scale-dependent response of local diversity, our study reveals important insights into how regional diversity translates into local diversity. Translations of regional diversity into local diversity have been thought to be different on islands and mainlands (Rosenzweig & Ziv 1999). On the mainland, regional diversity would translate into local diversity as observed in our data for fern diversity at a larger grain size of local diversity when compared to the grain size at islands. Contrary on islands, regional diversity would translate into local diversity as observed in our data at small spatial grain sizes. This shows that relations between regional and local diversity can not only be altered by different geographical settings (mainland vs. islands) but also altered by spatial scale.

Conclusions

In conclusion, we found that the two main factors of the ETIB, area and isolation, are strong predictors of fern diversity on islands at regional scales. The species pool has a scale-dependent influence on diversity and is unimportant at the local (α) scale where diversity appears to be saturated. At this scale, local variation in environmental conditions becomes a far stronger predictor of fern diversity. The lack of explanatory power of area and isolation at the local α scale is most likely due to the species saturation of communities. More generally, to make predictions about how regional processes may influence local assemblages, it is therefore important to take the scale-dependence of species pool effects into account and to acknowledge that these effects influence species diversity only down to the scale at which diversity becomes saturated.

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Chapter II.5

Differences in species-area relationships across land plants: a macroecological perspective

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revised version with additional co-author Péter Sólymos published in *Global Ecology and Biogeography*, 2014, **23**, 1275-1283, DOI: 10.1111/geb.12230

Abstract

Aim Although the increase in species richness with increasing area size appears as one of the few laws in ecology, the role of geographic isolation and intrinsic taxon features in shaping species-area relationships (SPARs) remains controversial. Based on a global survey of land plant floras across oceanic and continental islands and continents, we test the hypotheses that (i) geographic remoteness on oceanic islands results in significantly lower intercepts and higher slopes than in continental ones and continents; and (ii) the slope and the intercept of the SPARs gradually increase from bryophytes to pteridophytes to spermatophytes as a response to their differences in dispersal capacities.

Location 421 datasets distributed worldwide.

Methods Linear mixed effect models subjected to information-theoretic model selection were employed to describe variation in SPARs across gradients of geographic isolation (GEO) and dispersal capacities (TAXON), while controlling for the influence of realms (REALM) and biomes (BIOME).

Results The best random effect structure included both a random slope and a random intercept for TAXON, GEO, REALM and BIOME. The slope of the SPARs was higher in oceanic islands than in continental ones and continents, and higher in spermatophytes than in pteridophytes and bryophytes. The intercept exhibited the reverse trend.

Main conclusions Geographic isolation and taxon-specific traits cause differences in SPAR model parameters. Such differences in SPARs among land plant lineages challenge neutral ecological theories and, in particular, the idea that accumulation of species richness on islands is exclusively controlled by extrinsic factors, as implied, among others, by McArthur and Wilson’s equilibrium model of island biogeography. Taxon-specific differences in SPARs were, however, confounded by interactions with geographic isolation. This highlights the importance of applying integrative frameworks taking both geographic context and taxonomic idiosyncrasies into account in SPAR analyses.

Introduction

The increase in species richness (SR) with increasing area size, known as the species–area relationship (SPAR), has been recurrently reported in taxa as diverse as bacteria (Horner-Devine *et al.* 2004; Bell *et al.* 2005), plants (Gerstner *et al.* 2013; Lazarina *et al.* 2013), and animals (Storch *et al.* 2012). It therefore appears as one of the few laws in ecology (Dodds 2010), with fundamental implications for our understanding of global biodiversity patterns (Rosenzweig 1995). SPARs have typically been modelled by a power-law model (for review, see Triantis *et al.* 2012), $S = cA^z$. However, the ecological interpretation of variation in the model parameters, intercept (c) and slope (z), as well as the factors shaping SPARs remains an area of controversy (Triantis *et al.* 2012).

MacArthur and Wilson's equilibrium theory of island biogeography (ETIB, 1967) predicts that, due to the combined effect of extinction and low colonization rates on isolated islands, the slope of the SPAR increases with geographic isolation. As opposed to this prediction, however, empirical evidence failed to demonstrate significant differences in SPARs on continents, continental islands (including islands which are located on the continental shelf and may have been connected to continent during the Quaternary Ice Ages, and islands formed by ancient continental fragments), and oceanic islands, which are of volcanic origin, often more isolated and have never been connected to continents (Drakare *et al.* 2006; Sólymos & Lele 2012). Large, remote islands may not attain levels of SR predicted based on their area because immigration rates are very low on distant archipelagos (Weigelt & Kreft 2013), especially in taxa with poor dispersal capacities (Whittaker & Fernández-Palacios 2007). Although MacArthur and Wilson (1967) acknowledged the potential role of taxon-specific traits in shaping SPARs, the ETIB is a neutral model that relies on the dynamic equilibrium of colonization and extinction processes, but dismisses differences in life-history traits among species (Franzén *et al.* 2012).

Empirical evidence from metacommunity studies congruently pointed out that differences in dispersal limitation may alter the SPAR by modifying both colonization-extinction rates and community composition at local and regional scales (Hanski 1999; Ricklefs & Renner 2012; but see Aranda *et al.* 2013). Consequently, the explanatory power of the SPAR increases considerably when their slope is allowed to vary depending on taxon-specific differences in life-history traits (Franzén *et al.* 2012). Storch *et al.* (2012; but see Lazarina *et al.* 2013) further showed that SPARs for various vertebrate classes collapse into a single curve after the axes are rescaled, adjusting the area-axis to the mean range size of the species and the species-axis to the species richness of an area equal to the mean range size. Since dispersal ability has traditionally been perceived as a major driving force in the establishment and maintenance of large range sizes (Lowry & Lester 2006; but see Lester *et al.* 2007; and Iversen *et al.* 2013), this further implicitly points to the importance of life-history traits in shaping the SPARs. No differences in SPARs among oceanic island spore- and seed-producing land plant floras were, however, detected (Aranda *et al.* 2013), and the role of intrinsic taxon features, and dispersal capacity in particular, in determining SPARs remains controversial (Lester *et al.* 2007; Iversen *et al.* 2013). Surprisingly, few empirical studies have explicitly addressed whether species with contrasting dispersal traits differ in their SPARs (Franzén *et al.* 2012; Triantis *et al.* 2012), and whether the shape of SPARs varies between island and continental settings (Drakare *et al.* 2006; Kreft *et al.* 2008; Gerstner *et al.* 2013).

Land plants produce a range of diaspores, whose size (Wilkinson *et al.* 2012), number and morphology (Mehltreter *et al.* 2010; Hintze *et al.* 2013), stress tolerance (i.e. desiccation, UV intensity; van Zanten & Gradstein 1988; Löbel & Rydin 2010), and dispersal mode (Gillespie *et al.* 2012) determine their long-distance dispersal (LDD) capacity. In spermatophytes, the smallest seeds measure c. 0.05 mm in diameter (Arditti & Ghani 2000). However, most seeds considerably exceed the average size of spores produced by pteridophytes (0.02-0.13 mm; Chung & Chung 2013) and bryophytes (0.005-0.1 mm; Crum 2001), which is a critical condition for wind LDD (Wilkinson *et al.* 2012).

Within spore-producing plants, asexual diaspores are produced in great abundance and play a central role in the dispersal and establishment of bryophytes (Glime 2007), but their importance is comparatively negligible in pteridophytes (Mehltreter *et al.* 2010). In the latter, spores are, on average, larger than in bryophytes and, for species with only green spores, viability and tolerance to travel in wind currents are lower than for species with non-green spores due to their higher metabolic rate and consequently shorter viability, especially in harsh environments (Muñoz *et al.* 2004; Glime 2007; Mehltreter *et al.* 2010). Within bryophytes, mechanisms promoting spore release substantially differ among lineages. In liverworts and hornworts, spore dispersal is enhanced by hygroscopic movements of elaters. In mosses, the peristome ensures the gradual release of spores, increasing the likelihood of spores being widely distributed under different climatic conditions.

Based on the first comprehensive global survey of land plant floras, including hornworts, liverworts, mosses, pteridophytes, and spermatophytes, and using a linear mixed effect model (LMM) approach (Bunnefeld & Phillimore 2012) to detect differences in the SPAR shape and, if necessary, correct for taxon and/or area idiosyncrasies while controlling for environmental heterogeneity, we test here the following hypotheses: (i) geographic remoteness on oceanic islands results in significantly lower intercept and higher slope than in continental islands and continents; and (ii) the slope and the intercept of the SPARs is lower in bryophytes than in pteridophytes and spermatophytes due to their differences in dispersal capacities.

Methods

Compilation of species richness data

Species richness (SR) of hornworts, liverworts, mosses, pteridophytes (ferns and lycophytes) and spermatophytes (seed plants) at different spatial scales was recorded from a comprehensive literature survey at a different spatial scales ranging from single oceanic islands to entire political units (Text V.5.1). Species richness ranged from 0 to 51,220 species in spermatophytes, from 0 to 1,500 in pteridophytes, and from 1 to 1,731 in bryophytes (Table V.5.1). Addressing our two hypotheses, variation in the SPAR was explored depending on two factors, namely the taxonomic group (TAXON) and the geological system (GEO). We distinguished three different taxonomic groupings for the factor TAXON, namely: (i) seed- versus spore-producing plants (grouping A); (ii) spermatophytes, pteridophytes, and bryophytes (grouping B); and (iii) spermatophytes, pteridophytes, mosses, hornworts and liverworts (grouping C). For phylogenetic consistency, hornworts should have been analyzed separately. They are, however, a small group of only about 150 species worldwide whose diversity pales in comparison to the much more diverse liverworts (c. 6,000 species) and mosses (c. 10,000 species). The number of hornwort species in our dataset did not warrant separate analyses and, since hornworts exhibit a suite of functional vegetative traits and ecological features that are similar to those of liverworts, the data from the two groups were merged (hereafter referred to as liverworts).

Differences in geographic isolation and geological history were taken into account by the factor GEO, which included continents, continental islands (including continental-shelf islands and ancient continental fragments), and oceanic islands. The few cases of island groups with a mixed continental and oceanic origin (e.g. Japan and New Zealand) were included in the continental category. In total, information on SR of different taxonomic groupings and area size (AREA; in km^2) was collected for 421 operational geographical units (OGUs), including: 195 continental OGUs; 100 continental islands; and 126 oceanic islands (Text V.5.1). AREA (planar area; (Triantis *et al.* 2008) was adopted from the original reference if stated by the authors. Otherwise, AREA was derived from the UNEP Island Directory (Dahl 2004) or from encyclopedias. AREA ranged from 0.131 to 8,511,965 km^2 for continental landmasses, from 0.071 to 2,166,086 km^2 for continental islands, and from 1.3 to 103,000 km^2 for oceanic islands.

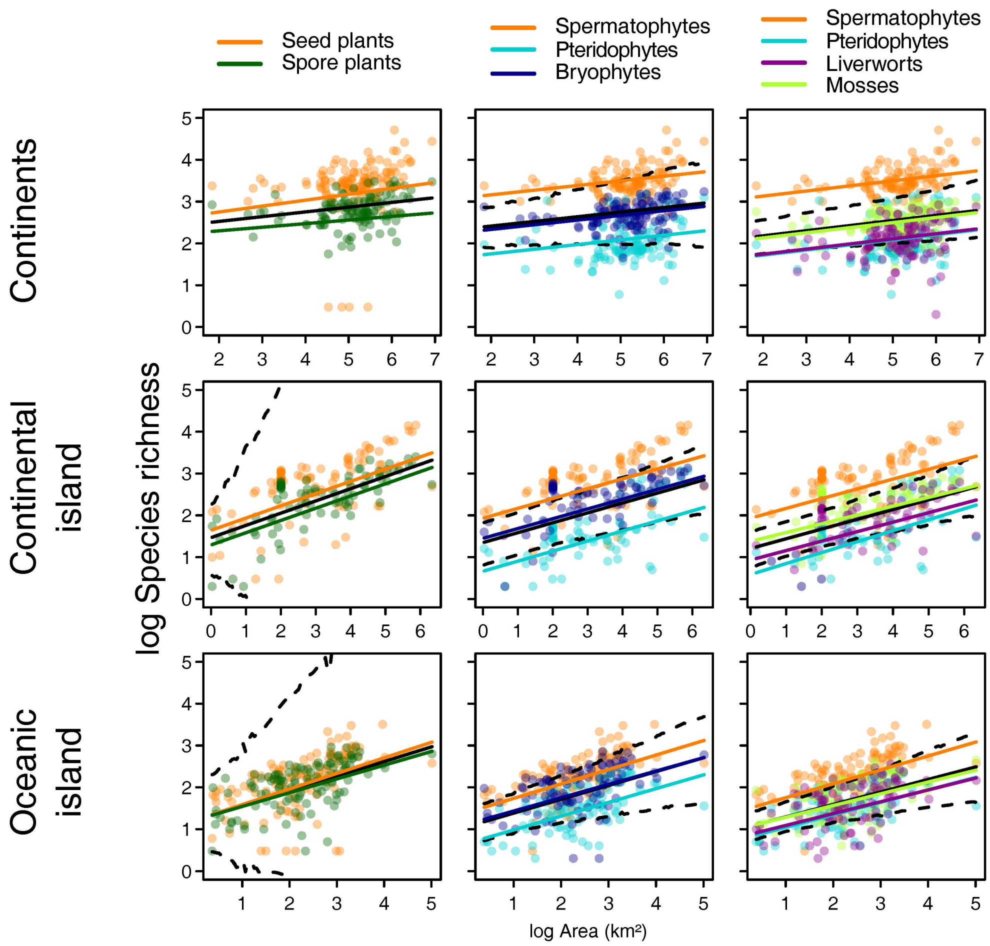

Figure II.5.1. Species-area relationships across land plants controlling for variation among taxonomic groups (TAXON), biomes (BIOME), and realms (REALM) within continents, continental islands and, oceanic islands (see Table II.5.3 for model description). The response variable, species richness of each taxon group per geological system, was log-transformed and explained by island area (log-transformed, km^2), the solid and dotted black lines representing average and confidence interval of the species-area relationships across land plants.

Two additional factors, biome (BIOME) and realm (REALM; Kreft *et al.* 2008) were also employed to control for differences in the SPAR parameters of the power model (c, z), caused by variation in macroclimatic conditions and biogeographic history (Drakare *et al.* 2006; Guilhaumon *et al.* 2008; Gerstner *et al.* 2013). Each of the 421 areas was assigned to one of 13 biomes (Tundra; Boreal forest-Taiga; Montane grasslands and shrublands; Temperate coniferous forests; Temperate broadleaf and mixed forests; Tropical and sub-tropical moist broadleaf forests; Tropical and sub-tropical dry broadleaf forests; Tropical and sub-tropical coniferous forests; Mediterranean forests, woodlands and scrub; Tropical and sub-tropical grasslands, savannas and shrublands; Temperate grasslands, savannas and shrublands; Deserts-Xeric shrublands; Flooded grasslands and savannas; Olson *et al.* 2001) and one of eight biogeographic realms (Afrotropics, Indo-Malaya, Nearctic, Neotropics, Palaearctic, Oceania and Australasia; Olson *et al.* 2001). We excluded the mangrove biome because of its limited extent, azonal character, global scarcity of available data, and the almost complete absence of bryophytes and pteridophytes in seawater environments.

Statistical analyses

To account for issues potentially arising from pseudoreplication (e.g. when manifold data points are gathered from the same archipelago or biological group), as well as statistical shortcomings related to the analysis of each taxon and geographic region separately (for review, see Bunnefeld & Phillimore 2012), a mixed effect modelling approach was employed to explore variation in the SPAR depending on the factors GEO and TAXON while controlling for the influence of BIOME and REALM. This approach takes advantage of LMMs (Zuur *et al.* 2009) for the analysis of clustered dependent data. LMMs are statistical models that incorporate both fixed (i.e. explanatory factors) and random effects. Random effects are used to control for pseudoreplication in the data while taking heterogeneity in the relationships between SR and AREA among regions and/or taxonomic groups into account. Instead of estimating coefficients separately for each geographic region and taxon, random effects are used to assess the variation of the parameters induced by the particularities of the areas and taxa under study (Zuur *et al.* 2009; Bunnefeld & Phillimore 2012; Patiño *et al.* 2013b).

A power law was applied after log10-transforming SR [log10(n+1)] and AREA. To facilitate the interpretation of the results and to decrease the complexity of the analyses, we ran two sets of analyses. We first explored the global effects of the factors GEO and TAXON. Second, we assessed the importance of the factor TAXON within each of the three geological settings, and of the factor GEO within each of the taxonomic groupings considered.

We subjected LMMs to information theoretic model selection to seek for the best combinations of explanatory variables for variation in SR (Zuur *et al.* 2009; Bunnefeld & Phillimore 2012). First, the best random effect structures, with the fixed effects considered (AREA), were selected using the Akaike Information Criterion corrected for small sample size (AICc, Burnham & Anderson 2002). The difference between the AIC_c of each model and the lowest AIC_c of all models, ΔAIC_c (Burnham & Anderson 2002), was used to identify the best random structure(s) for each taxonomic grouping. All models with a ΔAIC_c value < 2 were considered as having effectively equivalent levels of support (Burnham & Anderson 2002). We ran models allowing or not for all possible combinations of varying intercept and slopes across areas for the factors considered in the random effect structure (TAXON, GEO, REALM, BIOME).

In most best models for the three taxonomic groupings (A, B, C), random intercepts and random slopes of TAXON, GEO, REALM and BIOME were found. In a second step, we therefore

Table II.5.1. Factors included in the random effect structure controlling for variation in the species-area relationships across land plants due to differences among taxonomic groups (TAXON), geographic isolation (GEO), realms (REALM), and biomes (BIOME). Grouping: A = seed vs. spore-producing plants; B = spermatophytes, pteridophytes, bryophytes; C = spermatophytes, pteridophytes, liverworts, mosses. Liverworts include hornworts (see Methods). Only the best random effect structures (i.e. $\Delta\mathrm{AIC}_c < 2$) are shown; in black bold when the best model with $\Delta\mathrm{AIC}_c = 0$ included the random intercept and/or the random slope for TAXON and GEO. A 'blank field' indicates that the parameter was not included in a given model.

Random intercept				Random slope				**AIC**	**AIC_c**	**ΔAIC**	**$\Delta\mathrm{AIC}_c$**	**Grouping**
TAXON	**GEO**	**REALM**	**BIOME**	**TAXON**	**GEO**	**REALM**	**BIOME**					
	1	**1**	**1**	**1**	**1**	**1**	**1**	**699.34**	**699.68**	**0**	**0**	**A**
1	**1**	**1**	**1**	**1**	**1**	**1**		**872.07**	**872.32**	**0**	**0**	**B**
1		1	1	1		1	1	872.24	872.44	0.17	0.12	B
1	1	1	1	1		1	1	873.51	873.76	1.44	1.44	B
1	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1116.26**	**1116.49**	**0**	**0**	**C**

selected models with both random intercept and slope for all the factors considered in the random structure for comparison (TAXON, GEO, REALM, BIOME; the saturated random structure) to get all model parameters (coefficients) for each factor included in the SPAR. We initially included islands with 0 species to avoid biased estimates of *z*-values (Dengler & Oldeland 2010). The best random structure and the parameter coefficients were, however, very similar when excluding or including zeros in the different taxonomic groupings (results not shown).

All LMMs were fitted with the "lmer" function in the "lme4" library (version 0.999999-0) in R version 2.12 (R Development Core Team 2010), using restricted maximum likelihood for selecting the random effects structure and maximum likelihood for estimating the fixed effects. Significance of parameter estimates was assessed using the "languageR" library.

Results

A significant relationship between SR and area size (AREA) was consistently observed in the analyses controlling for variation in TAXON, GEO, REALM, and BIOME (Table V.5.2, Fig. V.5.1). Significant SPARs for most of the plant groupings were confirmed by the analyses focusing on the variation of the factor TAXON within each geological setting (Table V.5.3, Fig. II.5.1) and in the analyses focusing on the variation of the factor GEO within each taxonomic lineage (not shown).

Table II.5.2. Estimates of the species-area relationship model parameters (intercepts and slopes) for the taxonomic group (TAXON) and geological setting (GEO) factors, included in the best-fit random effect structure identified. Taxon groupings, as follows: A = distinguishing seed- and spore-producing plants; B = spermatophytes, pteridophytes and bryophytes; C = spermatophytes, pteridophytes, liverworts and mosses. Bold face indicates that the model parameter for a given factor was included in the best random effect structure (Table II.5.1).

Model	**Intercept (*c*)**	**Slope (*z*)**
Grouping A		
TAXON		
Seed plants	1.555	**0.321**
Spore-producing plants	1.555	**0.215**
GEO		
Continent	**1.932**	**0.177**
Continental island	**1.559**	**0.263**
Oceanic island	**1.176**	**0.363**
Grouping B		
TAXON		
Spermatophytes	**1.538**	**0.337**
Pteridophytes	**0.791**	**0.226**
Bryophytes	**1.384**	**0.224**
GEO		
Continent	**1.254**	**0.183**
Continental island	**1.251**	**0.263**
Oceanic island	**1.208**	**0.348**
Grouping C		
TAXON		
Spermatophytes	**1.595**	**0.342**
Pteridophytes	**0.885**	**0.223**
Liverworts	**1.067**	**0.195**
Mosses	**1.295**	**0.221**
GEO		
Continent	**1.511**	**0.173**
Continental island	**1.167**	**0.243**
Oceanic island	**0.953**	**0.320**

The shape of the SPARs was substantially affected by variation in the factors TAXON, GEO, REALM and BIOME, as evidenced by the inclusion of those factors in the best random effect structures (Table II.5.1). The *z*-values increased from about 0.2 on continents to 0.2-0.4 on continental and oceanic islands, whereas *c*-values exhibited the reverse trend. Intercepts and slopes were respectively higher and lower on continental islands than on oceanic islands (Table II.5.2; Fig. V.5.1). The *c*- and *z*-values of spermatophytes were higher than those of bryophytes (including liverworts and mosses), while the *c*-values of bryophytes were higher than those of pteridophytes. Slopes were lower when bryophytes were compared to pteridophytes, especially in the case of liverworts (Table II.5.2). There were only minor differences between mosses and liverworts, with the former showing slightly higher *c*- and *z*-values than liverworts.

In analyses performed at the scale of continents, continental islands, and oceanic islands respectively, a random intercept for TAXON was included in all of the best-fit models (Tables II.5.3 & V.5.4). The intercept values for each taxonomic group progressively decreased from continents, continental islands and oceanic islands (Table II.5.3, Fig. II.5.1). The single inconsistency was detected in pteridophytes (grouping B), where the *c*-value was higher on oceanic islands than on continental islands. Random slopes for TAXON were only included in the best random effect structure for oceanic islands (Tables II.5.3 & V.5.4), where *z*-values gradually decreased from spermatophytes to pteridophytes to bryophytes (Table II.5.3, Fig. II.5.1). Differences in slopes between liverworts and mosses were again negligible. In analyses performed within each of the lineages individually, a random slope for GEO was included in all of the best-fit models, but a random intercept was only included for spermatophytes (Table V.5.5).

Discussion

Our results showed that differences among the main lineages of land plants on the one hand, and among areas with contrasting levels of geographic isolation on the other, have a substantial impact on the shape of the SPAR, in line with our work hypotheses. Using the log-log space of the power function, the best model consistently included both a random slope and a random intercept for the factors GEO, TAXON, REALM and BIOME, evidencing their substantial impact in shaping the SPAR of land plants. This result reinforces the idea that spatial variation in SR is attributable to a suite of complementary factors that operate in combination, including life-history traits, climate and historical biogeography (Connor & McCoy 1979; Drakare *et al.* 2006; Guilhaumon *et al.* 2008; Franzén *et al.* 2012; Triantis *et al.* 2012).

The slope of the SPAR increased progressively from continents, over continental islands to oceanic islands, whereas the intercept exhibited the reverse trend for all the taxonomic groupings considered (Tables II.5.2 & II.5.3). The decrease in *c*-values and the increase in *z*-values with increasing geographic isolation are consistent with the equilibrium theory of island biogeography (MacArthur & Wilson 1967) and, in particular, with the expectation that SR decreases with geographic isolation due to lower colonization rates, whereas species turnover shows the reverse trend (Kreft *et al.* 2008; Weigelt & Kreft 2013; but see Connor & McCoy 1979). Our results support previous studies pointing to the decrease of *c*-values with increasing geographic isolation (Sólymos & Lele 2012; Triantis *et al.* 2012) and, more controversially, the increase in slope (but see Sólymos & Lele 2012; Triantis *et al.* 2012; but see Drakare et al. 2006).

The inclusion of the factor TAXON in the best-fit model across all geological settings demonstrated the existence of taxonomic-specific SPARs. This is not consistent with purely neutral theories which attempt to explain SR patterns in terms of common extrinsic immigration-speciation-extinction mechanisms (Hubbell 2001), as implied, among others, by MacArthur and Wilson's equilibrium model of island biogeography (1967). The finding of pronounced taxon-specific differences in SPARs is, however, in line with previous studies stressing the importance of non-neutral mechanisms in SPAR variation (Sólymos & Lele 2012; Triantis *et al.* 2012; but see Aranda *et al.* 2013).

Our study shows an increase of the slope from bryophytes to pteridophytes and then spermatophytes. The shape of the SPARs in bryophytes, and in particular, their low *z*-values, parallels that reported in microbes, which are typically flatter than those of macrobes (Bell *et al.* 2005; Green & Bohannan 2006; Hortal 2011). Bryophytes and, to a lesser extent, pteridophytes display a high wind LDD capacity (Medina *et al.* 2011; Schaefer 2011). This condition results in larger range sizes, lower compositional turnover, more homogenous community composition, and hence, flatter SPARs than in seed plants (Drakare *et al.* 2006; Lowry & Lester 2006). The almost identical *z*-values observed in mosses and liverworts suggests that diaspore size rather than differences in diaspore release mechanisms, accounts for the observed macroecological patterns in SR.

Progressively lower *z*-values from spermatophytes to pteridophytes and bryophytes further parallel differences in speciation mode due to their high LDD capacities (Mehltreter *et al.* 2010; Medina *et al.* 2011). In fact, a comparative analysis of the land plant floras on oceanic archipelagos revealed that anagenetic speciation (i.e. the gradual evolution of a new species after a founder event), contributed to 49% of bryophyte and to 40% of endemic pteridophyte species, but only to 17% of seed plant species (Patiño *et al.* 2013a). Exactly as the analogous increase of *in situ* speciation with geographic isolation results in higher *z*-values on oceanic islands than continental ones or continental landmasses (Kreft *et al.* 2008; Triantis *et al.* 2012), intrinsic low levels of diversification in spore-producing plants contributed to the lower *z*-values than in seed plants.

In line with the variation observed in *z*-values, bryophytes and pteridophytes exhibited lower intercepts than spermatophytes. This observation is consistent with the much lower global diversity and lower regional species richness per unit of area of bryophytes and pteridophytes as compared to the latter (Mutke & Barthlott 2005; but see Hortal 2011), also mirrored in the database compiled in the present study (see Table V.5.1). The low *c*-values of spore-producing plants might complementarily indicate that, being better adapted to shady and humid environments because of their drought strategy (Glime 2007; Mehltreter *et al.* 2010), mechanisms for establishing and persisting in small arid regions are more limited than in seed plants (Patiño *et al.* 2013a).

Table II.5.3. Estimates of the species-area relationship model parameters (intercepts and slopes) for the taxonomic group (TAXON) factor within continents, continental islands, and oceanic islands, included in the best-fit random effect structure identified. Taxon groupings, as follows: A = distinguishing seed- and spore-producing plants; B = spermatophytes, pteridophytes and bryophytes; C = spermatophytes, pteridophytes, mosses and liverworts. Bold face indicates that the model parameter for a given factor was included in the best random effect structure (Table V.5.4).

	Intercept (*c*)			Slope (*z*)		
Model	**Continent**	**Continental isl.**	**Oceanic isl.**	**Continent**	**Continental isl.**	**Oceanic isl.**
Grouping A						
Seed plants	**2.468**	**1.642**	1.214	0.141	0.292	**0.372**
Spore-producing plants	**2.127**	**1.292**	1.214	0.086	0.292	**0.328**
Grouping B						
Spermatophytes	**2.937**	**1.932**	**1.390**	0.111	0.235	**0.345**
Pteridophytes	**1.526**	**0.664**	**0.652**	0.111	0.240	**0.328**
Bryophytes	**2.110**	**1.451**	**1.113**	0.111	0.234	**0.318**
Grouping C						
Spermatophytes	**2.886**	**1.932**	**1.418**	0.121	0.233	**0.332**
Pteridophytes	**1.476**	**0.585**	**0.745**	0.121	0.261	**0.298**
Liverworts	**1.498**	**0.932**	**0.805**	0.121	0.226	**0.282**
Mosses	**1.887**	**1.378**	**1.001**	0.121	0.210	**0.281**

The signal of the geological setting and the taxonomic lineages on the shape of the SPAR was, however, confounded by an interaction between these two factors. This might explain why the only previous analysis of SPAR variation across land plants, although focused on oceanic islands but with a low statistical power due to the limited number of observations (n = 19; see Aranda *et al.* 2013), failed to evidence taxon-specific differences in SPARs. In fact, only slight differences in the SPAR slopes among mosses, liverworts, and pteridophytes were observed in the present study when the analyses was performed across geological settings, and were only revealed from analyses within oceanic islands. Such an influence of the factor GEO was evidenced by the inclusion of a random slope in the best-fit model for the factor TAXON in analyses performed at the level of oceanic islands, but not of continental islands or continental landmasses. This suggests that differences among groups of land plants in LDD capacities, but not short-distance ones, affect their spatial patterns of SR.

Indeed, as opposed to the idea that the high dispersal capacities of spore-producing plants mask any signal in their distribution patterns (Wolf *et al.* 2001), numerous bryophyte (Hutsemekers *et al.* 2010; Patiño *et al.* 2013c) and pteridophyte (De Groot *et al.* 2012; Chung & Chung 2013) species exhibit from a moderate to strong geographical structure in their local patterns of genetic variation that is reminiscent of that shown by many spermatophyte species (Linhart & Grant 1996). For instance, temperate bryophyte and tree species in Europe share similar post-glacial re-colonization patterns (Désamoré *et al.* 2012), further pointing to similarities in their global dispersal capacities at the intra-continental scale. At larger geographical scales, conversely, a typical feature of bryophyte distribution patterns is that many species exhibit trans-oceanic ranges (Shaw 2001). For example, 43% of the species of mosses found in North America are also found in Europe while 70% of the moss species found in Europe also occur in North America (Frahm & Vitt 1993). By contrast, only 6.5% of vascular plant species are shared between the North American and European floras (Qian 1999). Such patterns in bryophytes were primarily interpreted in terms of ancient vicariance (Schofield & Crum 1972). However, studies on the rates of molecular evolution between continentally disjunct species, molecular dating, and indirect measures of gene flow derived from population genetic statistics, all unambiguously point to LDD as the main driver of the disjunct distribution patterns of bryophytes (for review, see Vanderpoorten *et al.* 2010). In spermatophytes by contrast, the much lower proportion of trans-Atlantic disjunctions is still interpreted in terms of a balanced mixture of ancient vicariance and recent LDD (Kadereit & Baldwin 2012).

A second interaction between geological origin and taxonomic group was revealed through the absence of the intercept for the factor GEO when bryophytes (mosses and liverworts) and pteridophytes were analyzed independently, whereas this factor was included in the random structure in spermatophytes. This suggests that, in pteridophytes and bryophytes, the realized island carrying capacity does not decrease with geographic isolation because of declining colonization rates. The failure of geographic distance to account for SR patterns in spore-producing plants is consistent with previous studies (De Groot *et al.* 2012; Patiño *et al.* 2013b), where the contribution of this factor was substantially lower than that of factors accounting for environmental heterogeneity. These observations, along with the widespread distributions of bryophyte and pteridophyte species among islands within archipelagos (Mehltreter *et al.* 2010; Vanderpoorten *et al.* 2010), extremely reduced levels of endemism (Patiño *et al.* 2013a), and substantial allele sharing between islands and continents (Shepherd *et al.* 2009; Hutsemékers *et al.* 2011), reinforce the idea that oceanic barriers are not a major impediment for migration in the group (Mehltreter *et al.* 2010; Patiño *et al.* 2013b) and that, once airborne, spores randomly travel across various spatial-scale distances (Sundberg 2013).

Our results demonstrate that SPARs in land plants are shaped by extrinsic (geographic isolation) and intrinsic (taxon dispersal capacities) factors, challenging neutral theories. This highlights the importance of applying integrative frameworks taking both geological histories and taxonomic idiosyncrasies into account in SPAR studies, which has critical consequences for the use of the SPAR in conservation biology. Desmet and Cowling (2004) proposed that the *z*-value can be used to estimate the area size required to conserve a defined proportion of the local species pool. Given the differences in species accumulation rates among land plant lineages in different geographic areas demonstrated here, our results provide an objective approach to determine, in each case, the extent of the area size requested to reach this conservation target.

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Chapter II.6

Global patterns and drivers of phylogenetic assemblage structure in island plants

Patrick Weigelt, W. Daniel Kissling, Yael Kisel, Susanne A. Fritz, Dirk N. Karger, Michael Kessler, Samuli Lehtonen, Jens-Christian Svenning and Holger Kreft

Abstract

Due to their isolation, islands are ideal to investigate the processes that shape the phylogenetic structure of assemblages: dispersal, environmental filtering, and diversification. We study these processes across 393 islands and 37,041 vascular plant species (angiosperms overall, palms, and ferns) using dated phylogenies and data on source pool size, island isolation, geology, area, age, environmental heterogeneity, past and present climate, and biogeographic history. Together these factors explained more variation in phylogenetic assemblage structure for angiosperms and palms than for ferns. As expected, signatures of dispersal and environmental filters, and in-situ speciation differed among taxonomic groups according to their dispersal- and speciation-related traits and levels of phylogenetic conservatism. When accounting for species richness, phylogenetic diversity was negatively related to isolation for palms (indicating dispersal filtering and endemic radiations), but positively for angiosperms (indicating colonization by multiple lineages) and not at all for ferns. Also, different measures of phylogenetic assemblage structure captured traces of different speciation patterns (radiations in single lineages vs. speciation in several lineages). We argue that clade-specific differences idiosyncratically shape global plant diversity by filtering and speciation.

Introduction

Despite progress in our ability to map global biodiversity patterns and in linking them to environmental variables such as climate (Hawkins *et al.* 2003; Kreft & Jetz 2007), our understanding of the underlying processes lags behind (Currie *et al.* 2004; Ricklefs 2004). Considering phylogenetic relationships among species may help to disentangle the roles of species interactions, environmental filtering, dispersal, speciation, and extinction in shaping diversity (Cavender-Bares *et al.* 2009). Notably, linking contemporary and past environmental factors to phylogenetic patterns will enhance our understanding of the associated mechanisms, providing a long-term evolutionary perspective (Ricklefs 2004). Here, we test the global phylogenetic patterns on islands for signatures of the macro-scale processes dispersal filtering, environmental filtering and diversification (Cavender-Bares *et al.* 2009), and of regional biogeographic history.

Recent advances in identifying phylogenetic relationships of major extant clades (Bell *et al.* 2010) and in computing comprehensive phylogenies (Davies *et al.* 2004a; Lehtonen 2011) have triggered scientific progress in community ecology (Webb *et al.* 2002; Cadotte *et al.* 2010). At macro-scales, phylogenetic patterns in diversity have been described for terrestrial vertebrates (Davies *et al.* 2008; Fritz & Rahbek 2012), but not for other animal groups or plants. Underlying processes have been addressed by focussing on diversification and environmental filters (Davies *et al.* 2007; Davies & Buckley 2011, 2012), but the role of dispersal, has proven particularly difficult to assess (Davies *et al.* 2007; but see Kissling *et al.* 2012b; Eiserhardt *et al.* 2013).

Islands are important study systems for investigating not only the impact of diversification and environmental filtering, but also dispersal filtering on the phylogenetic composition of assemblages. Due to their isolated nature and often incompletely occupied niche space, limited colonization and evolutionary processes have led to disharmonic biotas (Kier *et al.* 2009; Gillespie *et al.* 2012). Islands harbour a disproportionately high number of endemic species (Kier *et al.* 2009), either evolved *in situ*, e.g. through adaptive radiations on oceanic archipelagos (Losos & Ricklefs 2009), or preserved relicts on old continental fragments (Cronk 1997). The loss of island species thus has far-reaching consequences on the conservation of our planet's evolutionary legacy. Most broad-scale studies on island biodiversity have so far focused on species richness (SR; Kalmar & Currie 2006; Kreft *et al.* 2008; but see, e.g., Stuart *et al.* 2012; Cabral *et al.* 2014a for turnover). However, there is evidence from few global studies focussing on amphibians (Fritz & Rahbek 2012) and palms (Kissling *et al.* 2012b) that islands show distinct phylogenetic patterns driven by their isolated nature.

Here, we provide a global test of the three main factors shaping the phylogenetic assemblage structure of vascular plants on islands: dispersal, environment, and in-situ speciation (Fig. II.6.1). Isolation entails that certain species do not reach particular islands due to an inability of long-distance dispersal (dispersal filtering, Fig. II.6.1) (Gillespie *et al.* 2012). If dispersal-related traits are not randomly distributed over the phylogeny, but related species tend to have similar dispersal abilities (phylogenetic trait conservatism; Cavender-Bares *et al.* 2009), dispersal filtering should lead to phylogenetically clustered island assemblages (Donoghue 2008). The degree of isolation determines the chance of dispersal to an island (MacArthur & Wilson 1967). The strength of the dispersal filter should hence be related to island isolation, geologic history, and the size and composition of the mainland species pool (Fig. II.6.1).

Secondly, only certain species can tolerate the environmental conditions of particular islands (environmental filtering, Fig. II.6.1) (Gillespie *et al.* 2012). If adaptations to environments are not randomly distributed over the phylogeny, but related species tend to inhabit similar environments (phylogenetic niche conservatism; Wiens *et al.* 2010), environmental filtering should lead to phylogenetically clustered island assemblages under certain environmental conditions (Cavender-Bares *et al.* 2009). Environmental heterogeneity and climate have been

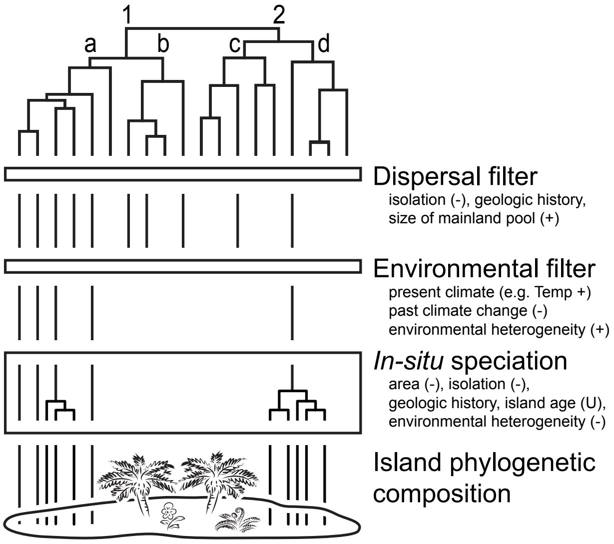

Figure II.6.1. Effects of dispersal and environmental filters as well as in situ speciation on the phylogenetic composition of island assemblages. If dispersal related traits and environmental adaptations are phylogenetically conserved, i.e. more similar between more closely related species, strong dispersal and environmental filters should restrict island colonization to certain clades and lead to phylogenetic clustering in island assemblages. Extinction due to environmental changes should further increase phylogenetic clustering. Recent speciation events and *in situ* radiations within island lineages should further increase phylogenetic clustering and decrease phylogenetic diversity in relation to SR. The strength of the dispersal and environmental filters as well as the probability of speciation on islands should be strongly related to physical, geologic, and bioclimatic island characteristics. In this hypothetical example, clade 1 represents a group of mainly good dispersers and clade 2 a group of mainly weak dispersers. Species in clades a and d share adaptations to the environmental conditions prevalent in the hypothetical island system, clades b and c do not. Speciation is more likely in the group of weak dispersers for two reasons: low levels of gene flow and incomplete niche filling. Symbols in parentheses behind environmental variables indicate the hypothesized relationships with the standardized effect size of phylogenetic diversity (PD_{es}): - negative, + positive, U u-shaped. geologic history is expected to affect dispersal and speciation in different directions, since volcanic islands provide novel environments and gene flow is low due to isolation, and continental islands have usually at some point experienced biotic exchange with the mainland. Continental fragments may even promote the preservation of relict lineages. Relationships are expected to be the opposite for the net relatedness index (NRI), a measure of phylogenetic clustering.

shown to be drivers of SR on islands (Kreft *et al.* 2008; Hortal *et al.* 2009) and can also be seen as environmental filters. The strength of environmental filtering should decrease with increasing environmental heterogeneity and should additionally be lowest under conditions where most lineages originated (e.g. tropical niche conservatism, Wiens & Donoghue 2004). Past climate change may have additionally caused extinctions of lineages that share certain preferences (Kissling *et al.* 2012b; Hawkins *et al.* 2013), although islands should be more buffered against such effects than mainlands (Cronk 1997).

Thirdly, cladogenesis on islands may create numerous closely related species (e.g. Hawaiian lobeliads; Givnish 2010), leading to low phylogenetic diversity (PD) in relation to SR (Fig. II.6.1) (Forest *et al.* 2007). Isolation promotes speciation by decreasing levels of gene-flow (Heaney 2000). Most importantly, however, the chance of speciation increases with area and topographic heterogeneity due to larger population sizes and intra-island reproductive isolation (Losos & Schluter 2000), depending on taxon-specific levels of gene-flow (Kisel &

Barraclough 2010). In addition, island geologic history is important for the assembly of island floras. Whereas continental fragments or shelf islands should harbour relatively saturated biotas from their formation onwards, volcanic islands or islands emerging from uplifted seafloor start out empty of species and thus provide more open arenas for immigration and speciation. Especially at the early stages, speciation rates are expected to be high until biotas become more saturated and niche space gets filled up (Whittaker *et al.* 2008). The effect of speciation on PD should hence be related to area, heterogeneity, isolation, geologic history and island age (Whittaker *et al.* 2008; Kisel & Barraclough 2010; Davies & Buckley 2011).

Here, we investigate environmental and historic biogeographic determinants of phylogenetic assemblage structure across 393 island floras at a global scale. We use vascular plants as a model group as they show a wide variety of dispersal modes, adaptations to climate and speciation modes. Specifically, we compare the deterministic roles of environments and biogeographic history on phylogenetic diversity and clustering of angiosperms in general, palms, and ferns (Box II.6.1). Addressing filtering and speciation effects on the phylogenetic composition of island assemblages, we test the following hypotheses (Fig. II.6.1):

Patterns and predictors vary among the taxonomic groups **(H1, group specifics)** due to differences in their dispersal ability, distribution patterns, diversification rates, and levels of phylogenetic trait and niche conservatism (Box II.6.1). The expected relationships (H2 - H4) are less pronounced for ferns than for angiosperms and palms due to their higher dispersal ability and the wide distribution ranges of most of their lineages. When accounting for SR effects, **(H2, dispersal filtering)** PD decreases with factors that increase chances of dispersal to islands (e.g. lower PD on more isolated islands); **(H3, environmental filtering)** PD is higher under environmental conditions that fit the bioclimatic requirements of more major lineages (e.g. higher PD under tropical climate); **(H4, *in situ* speciation)** PD is negatively related to factors increasing the probability of speciation on islands (e.g. lower PD on larger and more isolated islands). In addition to abiotic drivers, biogeographic history explains a major part of variation in phylogenetic assemblage structure **(H5, biogeographic history)**.

We provide the first assessment of phylogenetic assemblage structure of island biotas at a global scale, disentangling underlying drivers. Our analyses are based on a unique dataset of 118,062 occurrences of 37,041 species on 393 islands and the most up-to-date phylogenetic information available. We show that environmental and dispersal filtering processes and speciation, linked to physical and bioclimatic island attributes, influence phylogenetic diversity and structure of island floras. The underlying abiotic predictors and inferred mechanisms differ among taxonomic groups depending on their main dispersal- and speciation-related traits as well as levels of phylogenetic conservatism highlighting the importance of ecologic differences among groups in shaping global diversity patterns.

Box II.6.1. Ecological and biogeographical characteristics of angiosperms, palms and ferns relevant for the hypothesized relationships of phylogenetic diversity and structure with environmental factors (Fig. II.6.1).

Angiosperms overall. Dispersal modes in angiosperms range from wind dispersal to underground fruits that deposit seeds next to parent plants (Mabberley 2008). Some families show little variation in dispersal modes (Willson & Traveset 2000) and seed masses are often conserved among genera or families (Westoby *et al.* 1996). Many basal lineages also show conserved physiological tolerances and habitat affinities (Cavender-Bares *et al.* 2009) with half of the families being restricted to the tropics due to lacking cold tolerance (Donoghue 2008), rendering angiosperms an ideal model group to investigate filtering. Angiosperms show some classic examples of radiations on archipelagos (e.g. Hawaiian lobeliads; Givnish 2010) and single islands (Dypsis on Madagascar; Rakotoarinivo *et al.* 2013) and relict endemic island lineages even at the taxonomic rank of families (e.g. Amborellaceae on New Caledonia, Lowry II 1996; Lactoridaceae on Juan Fernandez islands, Bernardello *et al.* 2006).

Palms. The angiosperm family of palms (Arecaceae) is characterized by a strictly subtropical to tropical distribution with a strong temperature and precipitation-dependent diversity gradient increasing towards the inner tropics (Kreft *et al.* 2006; Kissling *et al.* 2012a). Most higher-level palm taxa lack adaptations to seasonality and cold due to their soft and water-rich tissue, an inability to undergo dormancy and a lack of frost tolerance (Eiserhardt *et al.* 2011; Kissling *et al.* 2012a). Palms have large seeds including the largest among all plants (Lodoicea maldivica; Fleischer-Dogley *et al.* 2011). Species with floating seeds or bird-mediated dispersal of fleshy fruits are capable of long-distance dispersal (Cuenca *et al.* 2008). However, many species are strongly dispersal limited (Fleischer-Dogley *et al.* 2011). For example, species with large fleshy fruits which are predominantly dispersed by non-volant mammals (Kissling *et al.* 2012b) should get filtered out with increasing island isolation. Accordingly, many higher-level palm taxa are restricted to certain biogeographic regions or islands (Eiserhardt *et al.* 2011). Palms show island radiations (Pritschardia on Hawaii; Givnish 2010; Coccothrinax and Copernicia on Cuba; Kissling *et al.* 2012b; Dypsis on Madagascar; Rakotoarinivo *et al.* 2013) and cladogenesis even on small islands (Howea on Lord Howe island; Savolainen *et al.* 2006).

Ferns. In contrast to angiosperms, few fern clades show comparable island radiations (but see Cibotium and Diellia on Hawaii; Tryon 1970; and Cyathea on Madagascar; Janssen *et al.* 2008) likely due to their high dispersal ability (Tryon 1970; Kisel & Barraclough 2010). Ferns have small wind-dispersed spores, and while there are mechanisms that promote cross-fertilization, most species produce bisexual gametophytes capable of self-fertilization (Smith 1972; Watkins Jr. & Cardelús 2012). Therefore, ferns show lower diversification rates and larger ranges than angiosperms, and speciation through hybridization and polyploidization makes up a large part of fern speciation events (Smith 1972; Kisel & Barraclough 2010). Hence, dispersal filtering and speciation should be of minor importance for fern phylogenetic diversity patterns on islands. However, environmental filtering might play an important role in ferns due to a strong phylogenetically conserved dependence on humidity (McAdam & Brodribb 2012). Only few fern lineages evolved adaptations to drought (Schuettpelz *et al.* 2007) which may be explained by eco-physiological constraints like the lack of active stomatal control (Brodribb & McAdam 2011), the need for water for sperm movement and a primitive water conducting system (Kessler 2010).

Methods

Species checklists

We assembled plant species lists from floras, checklists and online databases for a total of 393 marine islands. This dataset includes 375 lists for all flowering plants (Angiospermae), 386 lists for palms (Arecaceae) and 328 for ferns (Moniliformopses) including 32,446 angiosperm species, 1,143 palm species, and 3,689 fern species. All species names were matched with the Plant List (www.theplantlist.org) and the Taxonomic Name Resolution Service (tnrs.iplantcollaborative.org; see Text V.6.1 for details and references). Family assignment followed the Plant List, which for angiosperms largely corresponds to the Angiosperm Phylogeny Group (APG) classification III (2009). To match the taxonomic concepts of the fern phylogeny and to acknowledge recent advances in fern taxonomy, all fern names were additionally subject to a comprehensive and careful taxonomic check.

Phylogenetic trees

For angiosperms, we used the dated phylogeny from Bell et al. (2010) which includes 560 angiosperm species from 335 families (see Fig. V.6.1 for details). As an alternative, we used the angiosperm phylogeny from Davies et al. (2004), a supertree constructed from 46 source trees including 379 families and dated using one fossil-based age constraint. Below, we only show results for the phylogeny of Bell et al. (2010), because phylogenetic community metrics based on the two phylogenies were almost perfectly correlated (all $r > 0.98$, all $p < 0.001$, Table V.6.1). For palms, we used the complete and dated genus-level supertree from Baker and Couvreur (2013) (see Fig. V.6.2 for details). For ferns, we used a time-calibrated phylogeny from Lehtonen (2011) supplemented with additional data to have a taxonomically broad sample of 1,118 taxa including most extant fern genera (see Fig. V.6.3 for details).

For comparison between angiosperms and ferns, we pruned the two phylogenies to family level (for details see Figs. V.6.1 & V.6.3). For the calculation of phylogenetic community metrics, all species from the island checklists were added to the family-level phylogenies as tips in polytomies at 1/3 of the family stem node ages. To compare palm and fern phylogenetic patterns, we pruned the two phylogenies to genus level. Species were added to the genus level phylogenies as polytomies at 2/3 of the genus stem node ages (Kissling *et al*. 2012b). We chose

1/3 in family-level phylogenies to account for the higher discrepancy between stem node ages of families and species when compared to genera and species in the genus-level phylogenies. Comprehensive sensitivity analyses of the palm phylogeny show that the choice of age thresholds for polytomies does not qualitatively affect patterns and determinants of phylogenetic structure (Kissling *et al.* 2012b) because metrics are predominantly influenced by long branch lengths in older parts of phylogenies.

Phylogenetic community metrics

Calculation of the phylogenetic community metrics required a minimum number of two species per island, rendering 363 islands for all angiosperms, 71 islands for palms and 234 islands for ferns suitable for analyses. We calculated Faith's PD for each combination of island and taxonomic group as the total sum of unique phylogenetic branch lengths excluding the roots of the trees (Faith 1992). PD is inherently related to SR, as every new species adds an additional piece of evolutionary history to a species assemblage (Schweiger *et al.* 2008; Fritz & Rahbek 2012). To account for differences in SR among islands and the strong relationship between PD and SR (Table V.6.2), we calculated the deviation of PD from a global null expectation (PD_0) which was the mean value of PD calculated after randomly reshuffling the species names at the tips of the tree 1,000 times. We chose a global species pool in the null models because we were interested in global trends in environmental predictors of diversification and filtering rather than in within-region variation (compare Kissling *et al.* 2012b). Since the variance in the deviations from null expectations increases with SR, the deviation from the mean null expectation was divided by the standard deviation of the null-expectations (PD_{0sd}) to obtain the standardized effect size of PD:

$$PD_{es} = (PD - PD_0) / PD_{0sd}$$

To address phylogenetic structure, we calculated the net relatedness index (NRI; Webb *et al.* 2002), a standardized measure of mean pairwise phylogenetic distances (MPD) of species on an island, calculated as the deviation of MPD from the null model (MPD_0, 1,000 iterations) divided by the standard deviation (MPD_{0sd}) and then multiplied by -1 to reflect phylogenetic clustering instead of dispersion (hence, NRI is negatively related to PD_{es}; Table V.6.2):

$$NRI = -1\,(MPD - MPD_0) / MPD_{0sd}$$

Environmental predictors

Dispersal filter

We considered size of the mainland species pool, island isolation, and island geology as factors influencing plant dispersal to islands (Fig. II.6.1). For each island, we used the number of species in the nearest mainland grid cell from Kreft and Jetz (2007) as quantification of the number of species potentially available for island colonization. To represent island isolation, we used the surrounding landmass proportion from Weigelt and Kreft (2013), which is inversely related to the distance to the nearest mainland (Table V.6.3), but additionally accounts for island hopping via stepping stone islands and for the amount of source landmass (Weigelt & Kreft 2013). Island geology distinguished between continental shelf islands (likely mainland connection during the last glacial maximum), continental fragments (separated from continents due to tectonic movements), and oceanic islands (never connected to mainland).

Speciation

We considered island isolation and geology also as factors influencing speciation due to their effects on gene flow (Fig. II.6.1). In addition, we considered island age (My), area (km^2) and topographic heterogeneity (measured as elevational range in meters). We gathered the ages of 202 volcanic and uplifted seafloor islands from literature resources, as a proxy of time available for evolutionary processes. Island area and elevational range were taken from Weigelt et al. (2013a).

Environmental filter

As for speciation, we used elevational range as a proxy for topographic heterogeneity. As measures of contemporary climate, we considered mean annual temperature (°C), annual precipitation (mm), annual temperature range (°C), and variation in monthly precipitation to reflect present-day climatic conditions. To test for paleoclimatic effects, we used Late Quaternary climate change velocity (Sandel *et al.* 2011), i.e. the required speed to keep track with changing climate considering topographic complexity ($m\ y^{-1}$), since the last glacial maximum (21,000 y BP) for temperature. Climatic variables were taken from Weigelt et al. (2013a).

Statistical analysis

To account for expected non-linear relationships, we used generalized additive models (GAM) to examine the relationships between phylogenetic community metrics (PD_{es} and NRI) and environmental predictors. Area, surrounding landmass proportion and climate change velocity were $\log_{10}$-transformed. All predictors except geology were added as penalized regression splines with up to two degrees of freedom. Smooth terms in GAMs were penalized to prevent overfitting, but the minimum degree of freedom was larger than zero, making further model selection necessary in order to decide which terms to drop (Wood & Augustin 2002). We used Akaike's information criterion corrected for small sampling sizes (AIC_c) to select minimum adequate models (MAM) from all possible candidate models (Burnham & Anderson 2002).

We tested for spatial autocorrelation in response variables and in MAM residuals by comparing global Moran's I values for varying neighbourhood structures considering the $k = 1$ to 25 nearest neighbours and in distance classes of 500 km (Figs. V.6.4 & V.6.5). To account for spatial autocorrelation in model residuals, we applied spatial eigenvector filtering (Diniz-Filho & Bini 2005) (see Fig. V.6.4 for details). The model selection procedure was repeated including the set of spatial filters identified for the non-spatial MAM in all candidate models, and the new spatial MAMs as well as averaged models were used for representation of the results. We report pseudo R^2-values derived from a linear model of observed values and predicted values from the GAMs disregarding the spatial filters in the predictions to get an estimate of variation explained by the environmental predictors alone. We used cumulative AIC_c weights from all candidate models including a given variable as a measure of variable importance (Burnham & Anderson 2002).

We assessed the influence of island age on the phylogenetic composition of island floras using a subset of oceanic islands for which the age of emergence was available. We used the same model and spatial filter selection procedure for this subset ($n = 187$ for angiosperms, 31 for palms, 138 for ferns). Geology was not included in these models as all islands were of oceanic origin.

To test for regional effects of biogeographic history on present-day patterns of phylogenetic composition of island plants, we analysed the effect of floristic subkingdom membership (Takhtajan 1986). Again, we reran the model and spatial filter selection procedure including floristic subkingdom as additional predictor and performed model averaging.

All analyses were performed with R statistical software version 3.0.1 (R Development Core Team 2010) using R-packages *ape* (Paradis *et al.* 2004) for tree editing, *picante* (Kembel *et al.* 2010) for calculation of phylogenetic community metrics, *mgcv* (Wood & Augustin 2002) for

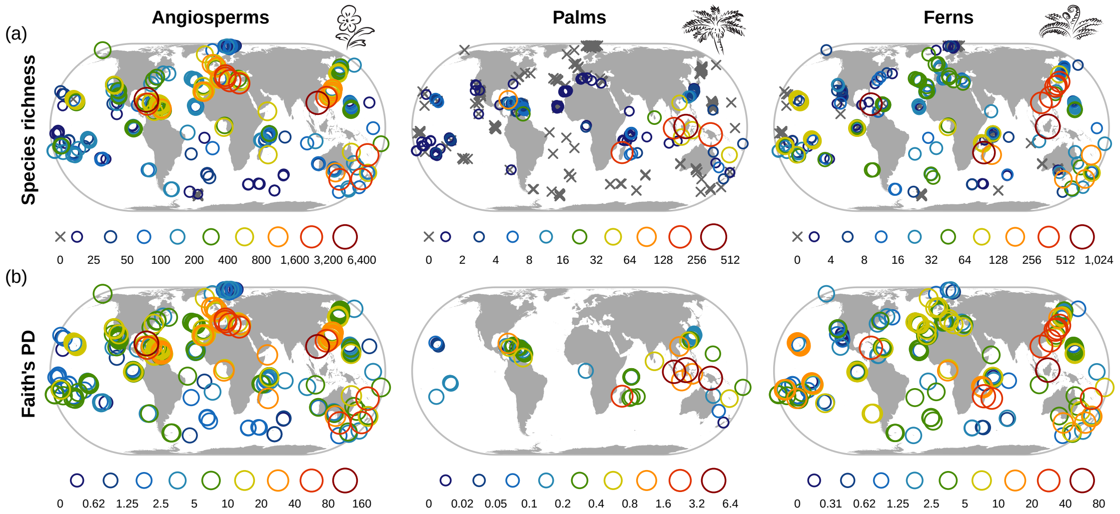

Figure II.6.2. Species richness (a) and Faith's phylogenetic diversity (PD) (b) of all flowering plants, palms, and ferns on islands worldwide. Numbers of species are shown for 375 islands for all angiosperms, 386 islands for palms (Arecaceae) and 328 islands for ferns. PD was calculated as the sum of all branch lengths the species of an island make up in the clades' phylogenies (Faith 1992) excluding the root of the phylogenetic trees, based on a dated family level phylogeny for angiosperms and on dated genus level phylogenies for palms and ferns. Species were added to tree tips as polytomies. PD is shown only for islands with at least two species of the focal group (363 islands for all angiosperms, 71 islands for palms only and 234 islands for ferns). Species richness is given in numbers of species, PD in billion years.

generalized additive modelling, *MuMIn* (Barton 2013) for model selection, averaging and calculation of variable importance, *vegan* (Oksanen *et al.* 2013) for generation of spatial eigenvectors, and *spdep* (Bivand *et al.* 2011) for spatial autocorrelation assessment.

Results

Patterns of phylogenetic assemblage structure

Phylogenetic diversity and species richness

Angiosperms occurred on 365 of 375 islands (97%) , palms on 170 of 386 islands (44%), and ferns on 255 of 328 (78%; Fig. II.6.2). Within each of the three plant groups, PD and SR showed similar patterns (Fig. II.6.2, Table V.6.2). The most species-rich islands also represented the most accumulated evolutionary history (e.g. Hainan and Cuba for angiosperms, Borneo for palms and ferns). PD and SR were strongly and positively related to each other in log-log space (all $r > 0.96$, $p < 0.001$) except for a slightly weaker relationship for palms ($r^2 = 0.83$, $p < 0.001$; Table. V.6.2). PD was highly correlated among groups (all $r > 0.7$, all $p < 0.001$; Table V.6.1).

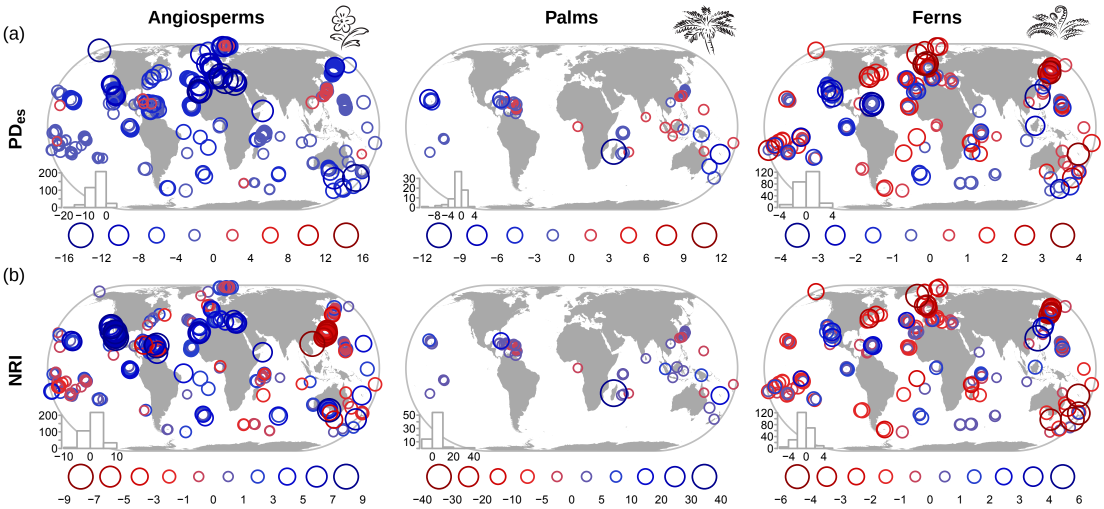

Figure II.6.3. Deviations of phylogenetic diversity (PD_{es}) (a) and structure (NRI) (b) from expectations based on species richness on islands for angiosperms, palms and ferns based on a dated family level phylogeny for angiosperms and on dated genus level phylogenies for palms and ferns. Species were added to tree tips as polytomies. PD was calculated as the sum of all branch lengths the species of an island make up in the clades' phylogenies (Faith 1992) excluding the root of the phylogenetic trees. The standardized effect size of PD (PD_{es}) was used to account for the positive relation between species richness and PD based on a null model randomly shuffling the species of the global species pool at the tips of the trees. Similarly the net relatedness index (NRI) is a standardized metric of mean pairwise distances among the species of each assemblage. Only islands with at least two species of the focal group are shown here (363 islands for all angiosperms, 71 islands for palms only and 234 islands for ferns). Embedded histograms give the frequency distributions of the mapped metrics.

Phylogenetic diversity as deviation from null expectations

Within the taxonomic groups, phylogenetic metrics accounting for SR (PD_{es} and NRI) were not significantly correlated with $\log_{10}$ SR for ferns (Table V.6.2). For angiosperms and palms however, PD_{es} was moderately negatively correlated to $\log_{10}$ SR (all $r > -0.4$, all $p < 0.01$) and for palms, NRI was positively correlated to $\log_{10}$ SR ($r = 0.59$, $p < 0.001$; Table V.6.2).

Values of angiosperm and palm PD_{es} were mostly negative (93% for angiosperms, 73% for palms) and NRI was mostly positive (69% for angiosperms, 80% for palms), i.e. PD and MPD were mostly smaller than expected by chance (Fig. II.6.2). Ferns showed less variation in the phylogenetic community metrics and a greater proportion of positive PD_{es} (59%) and negative NRI values (66%; Fig. II.6.2), indicating phylogenetic overdispersion. PD_{es} and NRI were strongly negatively correlated within each taxonomic group ($r < -0.84$ for all palms and ferns, $p < 0.001$). The relationship was weakest for angiosperms ($r = -0.56$, $p < 0.01$; Table V.6.2), presumably because some continental fragments like New Caledonia and Cuba showed high PD_{es} and high phylogenetic clustering (NRI).

Variable	Abbr.	Disp	Spec	Envi	Angiosperms	Ferns (family)	Palms	Ferns (genus)
Number of species in nearest mainland grid cell	***MLSR***	X			**1**	**1**	**0.92**	**1**
Geology (fragment, shelf, oceanic)	***Geol***	X	X		0.37	0.35	0.24	0.22
Surrounding landmass proportion (log$_{10}$)	***SLMP***	X	X		**1**	0.27	**0.98**	0.33
Island area (log$_{10}$; km^2)	***Area***		X		**1**	0.75	**0.97**	0.78
Elevational range (m)	***Elev***		X	X	0.52	**0.96**	0.29	**0.93**
Annual mean temperature (°C)	***Temp***			X	**1**	0.3	0.31	**1**
Temperature seasonality (range; °C)	***varT***			X	**1**	0.28	**0.92**	0.27
Annual precipitation (mm)	***Prec***			X	**1**	**0.98**	0.47	0.89
Precipitation seasonality (variation coefficient)	***varP***			X	0.71	0.42	**0.99**	0.83
Late Quaternary climate change velocity in temperature (log$_{10}$; m/a)	***CCVT***			X	0.34	**0.98**	0.37	0.27

Table II.6.1. Variable importance estimated from all possible multi-predictor generalized additive models for the standardized effect size of phylogenetic diversity (PD$_{es}$) of angiosperms, palms and ferns on islands in dependence on environmental predictors. Importance was assessed as cumulative Akaike's information criterion corrected for small sampling sizes (AIC$_c$) weights of all models a variable was included. Apart from the variables shown here, all candidate models included a set of spatial eigenvectors to account for spatial autocorrelation. For angiosperms, PD$_{es}$ was calculated based on a dated family level phylogeny, for palms based on a dated genus level phylogeny. PD$_{es}$ of ferns was calculated using phylogenies at both family and genus levels. Species were added to the tree tips as polytomies. All islands with at least two species of the focal group were included in models (n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns). Columns Disp (dispersal filter), Spec (speciation), and Envi (environmental filter) indicate which hypothesized mechanism on PD$_{es}$ the variables relate to. Values larger than 0.9 are printed in bold.

Among taxonomic groups, metrics accounting for the SR-PD relationship were at most weakly correlated ($|r| < 0.42$; Table V.6.1). For ferns, metrics based on the family-level phylogeny were strongly correlated to metrics based on the genus-level phylogeny ($r > 0.91$ for both metrics, $p < 0.001$).

Environmental predictors of phylogenetic assemblage structure

Environmental models of PD$_{es}$ explained up to 53% of variation for palms, 49% for angiosperms but only 18% for ferns (genus-level). Variation explained for ferns was slightly lower with the family-level phylogeny (15%; Table V.6.5). The statistical models for PD$_{es}$ and NRI were largely consistent. We therefore present results on PD$_{es}$ here and only report differences for NRI. For ferns, however, we do not discuss the differences due to the low explanatory power of all models (see Tables V.6.4 & V.6.6, Fig. V.6.6 for NRI).

Dispersal filter

Dispersal-related variables were especially important for angiosperm and palm PD_{es} (Table II.6.1). The proportion of surrounding landmass showed the hypothesized positive effect on palm PD_{es}, indicating a negative relationship between island isolation and PD_{es} (Figs. II.6.1 & II.6.4, Table V.6.5). For angiosperms, however, surrounding landmass proportion showed a significant effect opposite of expectations, i.e. increasing PD_{es} with increasing degree of isolation (Fig. II.6.4). For angiosperms and palms, island geologic history was significant in models of NRI but not in models of PD_{es} (Table V.6.5), with lowest values of NRI on continental shelf islands (Table V.6.6, Fig. V.6.6). Isolation and geologic history were unimportant for fern PD_{es} (Table II.6.1, Fig. II.6.4). The size of the mainland species pool had strong effects across all taxa (Table II.6.1), positively influencing PD_{es} of angiosperms and palms but negatively affecting fern PD_{es} (Fig. II.6.4).

Speciation

When accounting for all environmental co-variables, Island age did not have a significant effect on PD_{es} for any group (Fig. V.6.7). Based on model averaging, area was most important for angiosperms and palms (Table II.6.1). However, while PD_{es} showed the expected negative response to island area for angiosperms and palms, fern PD_{es} increased with area (Fig. II.6.4). In contrast to our expectations and results for PD_{es}, angiosperm NRI decreased with increasing area (Fig. V.6.6). For palms, PD_{es} decreased with increasing area only in areas larger than 100 km^2 (Fig. II.6.4). Only for ferns, elevational range had the expected importance and negative effect on PD_{es} (Fig. II.6.4, Table II.6.1). Just as for ferns, however, angiosperm NRI increased with elevational range (Fig. V.6.6).

Environmental filter

All present-day bioclimatic variables were important predictors for angiosperm PD_{es} (Table II.6.1). Angiosperm PD_{es} showed a u-shaped relationship to temperature, and a hump-shaped relationship to precipitation, and both variation variables (of temperature and precipitation) had positive effects (Fig. II.6.4). For palm PD_{es}, seasonality in both temperature and precipitation was most important (Table II.6.1). Palm PD_{es} showed a U-shaped trend with temperature range and a negative relationship with variation in precipitation (Fig. II.6.4). For ferns, temperature was most important for PD_{es} based on the genus-level phylogeny, while precipitation and climate change velocity were most important when using the family-level phylogeny (Table II.6.1). Fern PD_{es} (genus level) decreased with increasing temperature and increased with precipitation and precipitation seasonality (Fig. II.6.4).

Biogeographic history

Independent of the other predictors, Takhtajan's floristic subkingdoms explained 16.6% of the variation in PD_{es} for angiosperms, 7.5% for palms and 12.9% for ferns (family-level; Fig. V.6.8). For angiosperms, Takhtajan's floristic subkingdoms explained 30% of variation in NRI. Phylogenetic clustering (NRI) of angiosperm floras was highest in the Neocaledonian region and lowest on islands of the Australian, Boreal and Holantarctic regions after accounting for other environmental predictors. Interestingly, PD_{es} for angiosperms (and for ferns) was also highest in the Neocaledonian region. Lowest angiosperm and fern PD_{es} was found for the Madrean region. PD_{es} was lowest and NRI highest in the Madagascan region for palms. Palm PD_{es} was highest on New Zealand as part of the Holantarctic region.

Discussion

Environmental predictors of phylogenetic assemblage structure

We show that environmental factors drive phylogenetic community patterns on islands via dispersal filtering, environmental filtering and *in situ* speciation (Fig. II.6.1). Patterns in PD_{es} and NRI, and the strength and form of the relationships with environmental factors vary considerably among our clades (Table II.6.1, Figs. II.6.3 & II.6.4) with contrasting dispersal-related characteristics and main climatic adaptations (Box II.6.1). When accounting for SR, environmental predictors explained more variation in phylogenetic structure of global island floras for angiosperms and palms than for ferns (Table V.6.5), confirming H1. This indicates that dispersal filtering, environmental filtering and speciation differentially act as drivers of diversity among major taxonomic groups.

Dispersal filtering

In general, dispersal-related variables had strongest effects on angiosperm and palm PD_{es} (Table II.6.1), but contrary to our expectations (H2, Fig. II.6.1), angiosperm PD_{es} was positively

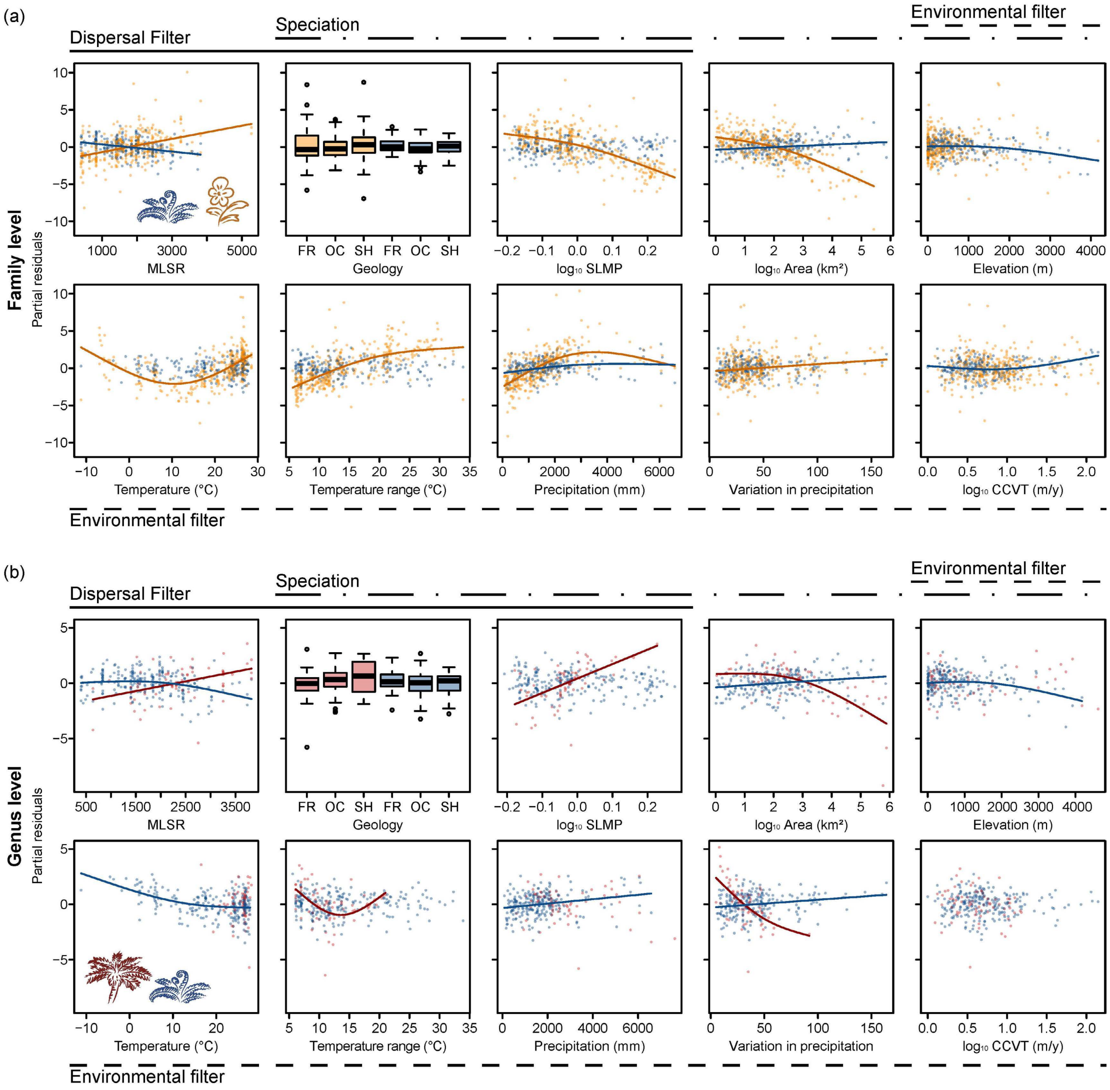

Figure II.6.4. Partial residual plots from averaged generalized additive models for the standardized effect size of phylogenetic diversity (PD_{es}) of angiosperms, palms and ferns on islands in dependence on environmental predictors. Models also included spatial eigenvectors to account for spatial autocorrelation. Regression lines are only shown if the variable was significant in the averaged model. In (a), PD_{es} was based on dated family level phylogenies of angiosperms (orange) and ferns (blue). In (b), PD_{es} was based on dated genus level phylogenies of palms (red) and ferns (blue). Species were added to tree tips as polytomies. Only islands with at least two species of the focal group are shown (363 islands for all angiosperms, 71 islands for palms only and 234 islands for ferns). Abbreviations follow Table II.6.1. Geologic island types: FR = continental fragment, OC = oceanic island (volcanic islands, atolls, uplifted sea floor), SH = continental shelf islands (mainly connected to the mainland during the last glacial maximum).

related to isolation (Fig. II.6.4). Angiosperms show a wide variety of phylogenetically conserved dispersal traits (Westoby *et al.* 1996) (Box II.6.1), leading to our expectation of a strong signal of dispersal filtering (Cavender-Bares *et al.* 2009) with increasing isolation. However, the phylogenetic composition of the most remote insular angiosperm floras indicates that immigrants stem from multiple biogeographic source regions with distinct evolutionary histories. The angiosperm flora of Hawaii e.g. is composed of elements from all circum-Pacific regions (Carlquist 1967). Isolated islands thus cannot be attributed to just one mainland source pool, leading to higher PD than expected. Furthermore, the variety of dispersal modes such as wind dispersal, epizoochory, endozoochory, and flotation contributing to the colonization of even remote archipelagos (Carlquist 1967) and convergent evolution (Cavender-Bares *et al.* 2009), render representatives from distinct angiosperm lineages possible immigrants. The negative effect of dispersal filtering seems therefore to be overlaid by a positive effect of a wide variety of well-dispersing clades with different biogeographic histories colonizing remote islands.

For palms, the positive effect of the proportion of surrounding landmass on PD_{es} is in line with H2. The strong dispersal filter observed here causes an absence of palm lineages of low dispersal ability leading to phylogenetically impoverished palm floras (Fig. II.6.4) and strong phylogenetic clustering on remote islands (Fig. V.6.6). These results are in line with results from Kissling *et al.* (2012b), highlighting strong dispersal limitation at high taxonomic rank in palms (Box II.6.1).

Island isolation proved unimportant for fern PD_{es} (Table II.6.1), which we attribute to the high dispersal ability of ferns (Smith 1972) (Box II.6.1). No signal of effective dispersal filtering was apparent due to the homogeneous distribution of small spore size among all major fern clades leading us to reject H2 for ferns. This is in line with recent findings on fern diversity in islands, indicating that the realized island carrying capacity does not decrease with geographic isolation for ferns (Kreft *et al.* 2010; Patiño *et al.* 2014). Although important for all taxa (Table II.6.1), the size of the mainland species pool was positively related to PD_{es} only for angiosperms and palms, further suggesting a stronger influence of immigration from the regional species pool compared to ferns.

Island geologic history had minor effects on PD_{es} for all groups (Table II.6.1, Fig. II.6.4). Angiosperm and palm NRI were significantly lower on continental shelf islands than on continental fragments and oceanic islands (Table V.6.6). If continental fragments and other oceanic islands were lumped and contrasted against shelf islands to acknowledge that both were not connected to mainland during the last LGM, PD_{es} was in addition significantly higher on shelf islands for palms ($p = 0.038$). Both indicates stronger dispersal filtering on oceanic islands as expected (Gillespie *et al.* 2012).

Speciation

The strong negative effect of island area on angiosperm PD_{es} suggests an important role of *in situ* diversification on large islands (H4) which is in line with increasing diversification rates with available area for mainland mammal clades (Davies & Buckley 2011). However, angiosperm NRI was also negatively related to island area. As NRI relies on mean pairwise phylogenetic distances, classic island radiations involving many speciation events within a single lineage lead to phylogenetic clustering, while the same number of speciation events in several distant lineages would rather lead to overdispersion. However, both scenarios would have similar effects on PD_{es} as each *in situ* speciation event adds one additional branch to Faith's cumulative measure of PD independent of its location in the tree. The negative effect of island area on PD_{es} therefore indicates an increase of *in situ* diversification with island area regardless of the number of radiations present, whereas the negative effect of island area on NRI indicates a decreased importance of single radiations relative to speciation events in several distinct lineages with increasing island area. This makes sense because the largest islands are all of continental origin harbouring floras from their formation on, leaving only little room for species-rich island-endemic radiations while supporting various lineages that might possibly diversify. Classic explosive island radiations, in contrast, mainly occur on volcanic archipelagos with smaller islands.

The largest palm radiations indeed happened on large continental islands (Box II.6.1). Hence, the strong negative effect of island area on palm PD_{es} and the positive effect on NRI support *in situ* diversification in form of radiation as a driver of island palm diversity patterns (Kissling *et al.* 2012b) which is also in line with strong dispersal limitation in palms (Fleischer-Dogley *et al.* 2011) and the observed negative effect of island isolation on palm PD_{es} and higher PD_{es} on continental shelf islands (Box II.6.1, Fig. II.6.4).

Island area played a minor role for fern PD_{es} (Table II.6.1). This is in line with H1 as high levels of gene flow in ferns hamper reproductive isolation even within large islands (Kisel & Barraclough 2010). Even though there is considerable endemism in ferns (70.8% endemic on Hawaii; Carlquist 1967), it is usually distinctly lower than for angiosperms (Carlquist 1967), and mostly evolved via anagenesis (Patiño *et al.* 2013a) not causing phylogenetic clustering. The slight positive relationship of PD_{es} and island area might be explained by target area effects (Whitehead & Jones 1969). A larger area may increase the chance to receive spores from a wider range of source areas with different biogeographic histories. Only ferns showed lower PD_{es} with increasing elevational range which might be attributed to rapid fern diversifications in tropical mountain regions (Kessler *et al.* 2011).

Our results do not support the assumed effect of isolation and geology on speciation for angiosperms (Fig. II.6.1). This might have two reasons: First, the variety of clades with different biogeographic histories that colonize remote islands (Carlquist 1967) lead to high PD_{es}; and second, cladogenesis also happens frequently on less isolated islands (Givnish 2010). Also, the proposed differentiation between relict lineages on continental fragments and radiations on volcanic islands did not create the expected results (Fig. II.6.4). In fact, there are examples for relict endemics on volcanic archipelagos (Fernández-Palacios *et al.* 2011) and for radiations on continental fragments (Morat 1993).

Surprisingly, island age of oceanic islands proved unimportant across all groups (Fig. V.6.7). We hypothesized a u-shaped relationship among PD_{es} and island age reflecting diversification mainly at early developmental island stages (Whittaker *et al.* 2008) and increasing PD_{es} at later stages due to accumulating evolutionary history. However, most oceanic islands and the accompanying radiations may simply be too young relative to the major plant lineages to create the hypothesized patterns.

Environmental filtering

Climatic variables were of great importance for angiosperm and palm PD_{es} and to a lesser degree also for fern PD_{es} (Table II.6.1), supporting H3. Biogeographic origin and phylogenetically conserved physiological constraints among the major clades within each group (Box II.6.1) determine which climatic factors act as environmental filters (Wiens & Donoghue 2004; Cavender-Bares *et al.* 2009). Accordingly, we found different environmental filters for the compared groups, supporting H1.

The increase of angiosperm PD_{es} with temperature above 10°C is in line with the tropical niche conservatism hypothesis (Wiens & Donoghue 2004) and recent findings for mean family ages of North American trees (Hawkins *et al.* 2013). The increase of PD_{es} with decreasing temperature below 10°C may be explained by fewer species at high latitudes which can be recruited from very distinct lineages (e.g. five species, five families on McDonald Island) and, possibly, lower diversification due to lower evolutionary rates under colder climates (Davies *et al.* 2004b; Davies & Buckley 2011). Just as cold tolerance, adaptations to drought may be conservative rather than convergent among many lineages (but see, e.g., the multiple convergent evolution of crassulacean acid metabolism, Keeley & Rundel 2003) as indicated by a strong positive relationship between PD_{es} and annual precipitation below 3,000 mm annually (Fig. II.6.4). In this context the positive relationship among PD_{es} and seasonality in both temperature and precipitation is rather counterintuitive. However, significant collinearity among annual means and seasonalities hampered interpretation.

For palm PD_{es}, seasonality in temperature (mean temperature for NRI) and precipitation were the most important climatic factors (Table II.6.1), in line with phylogenetically conserved adaptations to drought and low temperatures in palms (Box II.6.1). In fact, only one subfamily (Coryphoideae) extends beyond the outer tropics (Eiserhardt *et al.* 2011). Our results hence provide support for a strongly conserved tropical niche of palms caused by physiological constraints (Eiserhardt *et al.* 2011; Kissling *et al.* 2012a) (Box II.6.1).

Similarly, most fern lineages are restricted to humid climate (Kessler 2010) (Box II.6.1). Consequently, the positive relationship of PD_{es} with precipitation for ferns (Fig. II.6.4) was to be expected. Globally, fern diversity declines more strongly along aridity and coldness gradients than angiosperm diversity (Kreft *et al.* 2010), suggesting that ferns are evolutionary less adaptable. Here, drought acts as a filter and leads to phylogenetically impoverished fern floras on dry islands supporting that adaptations to drought are highly conservative in ferns.

The only relationships of PD_{es} to Late Quaternary climate change velocity for temperature (*CCVT*) emerged for ferns at family level. The lack of relationships between *CCVT* and PD_{es} of angiosperms and palms indicates an overall weak effect of Late Quaternary climate change driven extinctions on island PD patterns, which is in line with findings for palms (Kissling *et al.* 2012a). Instead it suggests that extinctions due to changing climate happened to species rather randomly distributed over their phylogenies and not within clades of common phylogenetically conserved characteristics, contrasting findings for South American and African palms.

Biogeographic history

Especially for angiosperms, Takhtajan's floristic subkingdoms accounted for a substantial proportion of variation explained in PD_{es} and NRI after considering environmental predictors ($r^2 = 0.30$ for angiosperm NRI; Table V.6.6, Fig. V.6.8), indicating a significant non-deterministic role of regional biogeographic history for shaping today's PD patterns on islands. Exceptionally high PD_{es} in Indomalesia can for example be explained by the high number of ancient lineages in South East Asia, one of the major centres of development of higher plants and preservation of ancient lineages (Takhtajan 1986). Low values in the Madrean region on the other hand, a region also characterized by a distinct flora including endemic families (Takhtajan 1986) was unexpected. However, Madrean endemic families are largely absent from the considered islands (California Channel Islands, Sea of Cortez islands).

The flora of New Caledonia, a floristic subkingdom according to Takhtajan (1986), stuck out as phylogenetically very diverse while having a high degree of phylogenetic clustering, and this could not be explained by environmental predictors (Fig. V.6.8). As the most isolated continental fragment (separated from Australia some 65 My ago), New Caledonia harbours many relict endemic lineages (Morat 1993), including the monospecific Amborellaceae, sister to all other extant angiosperms (Bell *et al.* 2010) which alone added c. 200 million years to New

Caledonia's PD. On the other hand, New Caledonia is an arena of massive adaptive radiations (Morat 1993) causing the high NRI value.

Limitations

Interactions at community level

We did not consider species interactions, although they may affect the phylogenetic assembly of island floras, especially at small spatial scales (Cavender-Bares *et al.* 2009). For example, the presence or absence of pollinators or mycorrhizal symbionts or the presence or absence of closely related competitors may decide over successful or not establishment of colonizers. Sometimes the roles of evolutionary and community ecologic aspects may be difficult to disentangle. For example, the negative effect of island area on angiosperm NRI for small islands (Fig. V.6.6) may depend on density dependent interactions rather than diversification mode, which should be more relevant for larger islands.

Differences among groups

The compared taxonomic groups differ considerably in age, number of species and major clades, and the number of islands inhabited (see Fig. V.6.3 for comment on resolution of phylogenies). Our hypotheses on dispersal and environmental filtering as drivers of PD patterns presume phylogenetic conservatism in traits which is assumed to vary with phylogenetic scale. The more of the tree of life is encompassed, the more conservative the traits should be (Cavender-Bares *et al.* 2009). However, if traits of clades of different biogeographic regions have converged, conservatism may diminish (Cavender-Bares *et al.* 2009), hampering comparisons among phylogenies. Indeed, our results help to understand patterns arising from different levels of trait conservatism. The environmental models explained varying proportions of variance for angiosperms, palms and ferns (Table II.6.1) indicating differences in both predominant trait characteristics and levels of trait conservatism. Furthermore, the fern phylogeny encompassed a similar time span like the angiosperm phylogeny and an intermediate number of species compared to angiosperms and palms (Figs. V.6.1 & V.6.3). In contrast to common beliefs, fern diversity is not older than angiosperm diversity but the largest ferns diversified in response to diversifications in angiosperms (Schneider *et al.* 2004). Differences in importance of filtering and diversification can therefore directly be linked to dispersal-related group characteristics.

Conclusions

Island biota are particularly threatened, by biological invasions, habitat loss, and changing climate (Kier *et al.* 2009; Kueffer *et al.* 2010; Wetzel *et al.* 2013). However, setting conservation priorities among thousands of islands is difficult. We caution against the use of PD as a surrogate of conservation value for island ecosystems (for review see Winter *et al.* 2013). We show that PD_{es} decreases with environmental factors that promote *in situ* diversification and hence endemism on islands (also see Forest *et al.* 2007; Isambert *et al.* 2011). Measures incorporating range sizes or rarity of species and phylogenetic uniqueness (Rosauer *et al.* 2009; Cadotte & Jonathan Davies 2010), may help to account for both phylogenetic history and rarity.

We show that environmental and dispersal filtering processes generate a strong signal in the phylogenetic structure of island assemblages and that different phylogenetic community measures capture signatures of different speciation patterns. Biogeographic history further plays an important role in shaping phylogenetic island assemblages. We argue that the mechanisms that shape the phylogenetic structure of island assemblages vary in importance among taxonomic groups depending on their main dispersal- and speciation-related traits as well as on levels of phylogenetic trait and niche conservatism. Our findings provide insight into how plant diversity of the considered plant groups on islands originates from immigration and diversification and adds an evolutionary perspective to macroecological models of island diversity. Considering clade-specific differences is hence important to understand global plant diversity patterns.

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Part III

Synopsis

1. Introduction

Islands have attracted attention since the early beginning of biogeographic research (Wallace 1880), evoking some of the most influential theories in ecology and evolution (Darwin 1859; MacArthur & Wilson 1967). Physical island attributes, like the well-defined area, discrete delimitation and isolated nature render islands suitable as ecological model systems (Whittaker & Fernández-Palacios 2007). However, island biogeography has mostly been restricted to some iconic archipelagos, and has not acknowledged the full variety of the world's islands' abiotic characteristics and of their biotic assemblages. Only about 5% of the Earth's land area belongs to islands, but their number exceeds 100,000, (depending on threshold size) and most of them are small, hampering the compilation of standardized data and comprehensive analyses.

In this thesis, I provide a rigorous and comprehensive bioclimatic and physical characterization of the world's islands (Chapter II.1) and investigate how island characteristics influence the diversity of island floras (Chapters II.2 - II.6).

Despite the long-known importance of island isolation as a driver of immigration and speciation (MacArthur & Wilson 1967), the roles of different aspects of isolation like stepping stone islands, surrounding landmass, wind and ocean currents, and climatic similarity among islands and mainlands have only been addressed in a few case studies (Muñoz *et al.* 2004; Price 2004; Diver 2008), rather than in a comprehensive, comparative manner (Chapter II.2). Islands are often spatially organized in an archipelagic context. The composition of island biotas is influenced by neighbouring islands, and the diversity of archipelagos depends on the biotas of their constituent islands. The effects of the spatial arrangement of archipelagic islands on aspects like the diversity of entire archipelagos (γ), the mean diversity of their constituent islands (α), or turnover among their islands (β) have not yet been addressed (Chapter II.3). Island area, isolation and macroclimate explain plant species richness well at the island level (MacArthur & Wilson 1967; Kreft *et al.* 2008). However, it is unclear to what degree physical island characteristics predict species richness at a local (plot-level) scale. With decreasing spatial grain from island to plot level, the importance of local environmental conditions may increase (Chapter II.4).

Major plant groups differ in dispersal abilities and levels of gene flow, speciation rates and adaptations to climate (Donoghue 2008). Physical characteristics of islands may hence affect different groups of organisms in different ways. The species-area relationship (SPAR), by which species richness increases with focal area (Triantis *et al.* 2012), should vary in strength and shape among groups, but recent analyses have shown unexpectedly homogeneous SPARs across Macaronesian land plant groups (Aranda *et al.* 2013) leaving this an open question (Chapter II.5). In the last decade, the phylogenetic history of global diversity patterns has attracted increasing scientific interest (Ricklefs 2004). Traits related to dispersal, gene-flow and adaptations to climate are often more similar among closely related species than expected by chance (phylogenetic trait and niche conservatism; Donoghue 2008; Cavender-Bares *et al.* 2009). Environmental and dispersal filtering mechanisms and *in situ* speciation may hence lead to phylogenetically clustered assemblages (Cavender-Bares *et al.* 2009; Kissling *et al.* 2012b). Thanks to their discrete and isolated nature, islands serve as ideal model systems to investigate the effects of environmental characteristics related to immigration, establishment, speciation and extinction on phylogenetic diversity (PD) patterns and assembly structure (Chapter II.6), adding an evolutionary perspective to macroecological island research.

The chapters of this thesis address two major aspects of the overarching question: what drives diversity patterns of island floras? First, I focus on past and present bioclimatic and physical island characteristics (with emphasis on the spatial structure of islands and archipelagos) as drivers of plant diversity patterns (all chapters); and second I focus on taxon-specific trait-related differences in the response of diversity patterns to abiotic factors (Chapters II.5 & II.6).

I provide a rigorous and standardized bioclimatic and physical characterization of the world's islands for island research and conservation (Chapter II.1). Using ordination and clustering techniques, I characterize the world's islands in a multidimensional environmental space and offer a dataset to bring forward macroecological and evolutionary island research. Specifically, I calculate physical characteristics - island area, distance to the nearest mainland, proportion of surrounding landmass, maximum elevation, and connection to mainland during the last glacial maximum (LGM) - using global data on administrative boundaries (gadm version 1, Hijmans *et al.* 2009) and digital elevation and bathymetry models (e.g. www.ngdc.noaa.gov/mgg/global/) for 17,883 of the world's islands larger than 1 km². I further use annual means and variability in temperature and precipitation from WorldClim (Hijmans *et al.* 2005) and calculate climate change velocity in temperature since the LGM, i.e. the required speed to keep track with climate change under consideration of topographic heterogeneity (Sandel *et al.* 2011).

I use the data from Chapter II.1 to provide global predictions of insular vascular plant species richness building on the statistical models in Kreft *et al.* (2008). Species numbers for training the model are partly taken from Kreft *et al.* (2008) and partly derived from a newly compiled database of 1,295 island plant checklists (Fig. I.3.1). The database includes c. 45,000 native vascular plant species. In contrast to existing datasets on island plant diversity, this is the first global and most comprehensive one including actual species identities, enabling me to investigate species turnover among islands and phylogenetic diversity patterns at a global scale.

In Chapter II.2, I address the roles of different aspects of island isolation in determining insular species richness. I compare ecologically meaningful metrics of island isolation and quantify their relative importance in determining vascular plant species richness. I hypothesize that the proportion of variation explained by isolation can be increased by considering large source islands, stepping stones, climatic similarity, wind and ocean currents and the area of surrounding landmasses, as opposed to considering only the commonly used metric of distance to the nearest mainland. I develop a set of 17 isolation metrics in 68 variations representing the above mentioned aspects of island isolation and evaluate their explanatory power for vascular plant species richness for 451 islands worldwide in a multi-predictor context based on richness data and statistical models in Kreft *et al.* (2008).

In Chapter II.3, I expand the perspective from single island isolation to inter-island spatial arrangement in archipelagos. I investigate α, β, and γ diversity of vascular plants on 23 archipelagos worldwide in dependence on biogeographic predictors like area, isolation and age, bioclimatic predictors, and intra-archipelagic spatial predictors. I hypothesize that α is mainly related to biogeographic and climatic determinants, that β is mainly driven by intra-archipelagic spatial structure, and that γ is mainly driven by indirect effects, i.e. through biogeographic, climatic and intra-archipelagic drivers that act via the α and β components. I develop a set of predictors describing the intra-archipelagic spatial structure of each archipelago, including mean inter-island distance, connectivity, total archipelago area, range in island areas, and the environmental volume occupied by an archipelago’s islands in the global bioclimatic and physical principal component analysis from Chapter II.1. I use multi-model inference to assess variable importance in linear multi-predictor models and structural equation models to test for the hypothesized indirect effects.

In Chapter II.4, I focus on scale effects on relationships between insular species richness and abiotic factors. I test whether the main physical island attributes considered by the equilibrium theory of island biogeography by MacArthur and Wilson (ETIB; 1967), i.e. area and isolation, serve to explain species richness at the plot level. I hypothesize that area and isolation are strong predictors of species richness only at large grain sizes and that their effects are diluted at small grain sizes (plot level) where local environmental conditions set an upper limit to species diversity and communities are saturated. I use field data on fern species richness in mountain forest plots on twelve islands in Indonesia and the Philippines (Karger 2013) and test for the effects of area, isolation, macroclimate and local environmental conditions on species richness at varying grain sizes from plots to entire islands using simple linear models and relative importance metrics.

In Chapter II.5, I address whether major land plant groups differ in their SPAR on islands and continental settings as a result of group-specific differences in dispersal ability. This adds a new perspective to my thesis as I compare ecological patterns among groups differing in their functional characteristics. I hypothesize that the geographic remoteness of oceanic islands results in SPARs with a lower intercept and a higher slope than SPARs on continental islands, which again show a lower intercept and higher slope than SPARs of continental areas. I further hypothesize that the slope and the intercept gradually increase from bryophytes to pteridophytes to spermatophytes. I apply a linear mixed effects modelling approach to describe variation in species richness in dependence on area across geological systems and taxonomic groups.

In Chapter II.6, I carry on the cross-taxon comparison and investigate how dispersal and environmental filtering in combination with *in situ* speciation affect the phylogenetic structure of island assemblages. I hypothesize that, when accounting for species richness effects, PD decreases with environmental factors that increase chances of dispersal to islands, PD is higher under environmental conditions that fit the bioclimatic requirements of more major lineages, and PD decreases with factors increasing the probability of *in situ* speciation on islands. I expect the relationships to be less pronounced for ferns than for angiosperms and palms due to their higher dispersal ability, wide distribution ranges and frequent speciation through hybridization and polyploidization (Kessler 2010). I investigate PD based on dated phylogenies for 393 islands and 36,297 species using deviations from null expectations in phylogenetic diversity and structure of island floras in relation to island area, isolation, geologic setting, island age, environmental heterogeneity, past and present climate, size of the source pool, and biogeographic history using generalized additive models.

2. Results and Discussion

The individual chapters of my thesis show how different aspects of island environments (e.g. past and present climate or the spatial island setting) affect different aspects of insular diversity (species richness, turnover, phylogenetic assemblage structure) at different scales (archipelago, island and plot-level) and for different major plant groups (e.g. bryophytes, ferns, seed plants).

The global island characterization (Chapter II.1) quantitatively confirms that islands differ from mainland areas in their bioclimatic and physical characteristics. Islands are, on average, significantly cooler, wetter and less seasonal than mainlands. Due to their limited area, they show less topographic heterogeneity. Wet temperate climates are more prevalent on islands supporting the occurrence of temperate rainforests, one of the rarest ecosystems on Earth (Olson & Dinerstein 2002). The main physical differences between islands and mainlands are the boundedness and remoteness of islands, defined by their position relative to other islands and the mainland.

I show that a thorough circumscription of the physical spatial characteristics of islands and archipelagos helps to understand their biota. Isolation is the second most important factor after area determining vascular plant species richness on islands (Chapter II.2). A model including the proportion of surrounding land area as the isolation metric has the highest predictive power, highlighting the importance of surrounding landmass as a source of constant immigration and an accompanying ‘rescue effect’ (Brown & Kodric-Brown 1977). These results are in line with findings at smaller spatial scales (Diver 2008) and for habitat islands (Fahrig 2013). Also, accounting for stepping stones, large islands as source landmasses and climatic similarity increases the explanatory power of isolation for species richness. I further show that isolation is less important on large islands, where *in situ* diversification counteracts the negative effect of isolation on immigration (Kisel & Barraclough 2010).

At archipelagic scales, intra-archipelagic spatial structure, particularly the mean inter-island distance and the range in island areas, turns out to be important for β diversity and, through β, for γ diversity of vascular plants (Chapter II.3). γ diversity is predominantly determined by indirect abiotic effects via α and β, with β being the more important component. Mechanisms like adaptive radiations (Losos & Ricklefs 2009), taxon cycle dynamics (Ricklefs & Bermingham 2002) and island-hopping (Gillespie & Roderick 2002) are linked to β diversity on archipelagos and are therefore driven by the intra-archipelagic spatial structure. These findings again highlight the importance of physical island characteristics, in this case describing the spatial location of islands relative to each other, for insular diversity patterns and indicate the necessity to consider islands in an archipelagic context in island research and conservation measures.

The importance of physical island characteristics on diversity gradually decreases with spatial grain size (Chapter II.4). Consistent with MacArthur and Wilson's ETIB (1967), I find strong correlations of area and isolation with fern species richness only at the island level. At the plot level, diversity is mainly driven by local environmental conditions, rather than by characteristics of the whole island. Local diversity is more saturated than diversity at large grain sizes, limiting the number of species that can migrate into local communities from the regional species pool (Fox & Srivastava 2006). To make predictions about local diversity on islands it is hence important to take the scale-dependence of species pool effects into account.

The comparative analyses reveal clear differences among major plant groups in the responses of species richness and phylogenetic diversity patterns to environmental drivers (Chapters II.5 & II.6). The linear mixed effect modelling approach enables us to reveal an increase in SPAR slopes from continents to continental islands to oceanic islands, and from bryophytes to pteridophytes and to spermatophytes (only for oceanic islands). Intercepts decrease from continents to continental islands to oceanic islands and from pteridophytes to bryophytes and to spermatophytes (Chapter II.5). These results are consistent with expectations based on the different long-distance dispersal capacities and dominant speciation modes of the considered plant groups, and on the degree of isolation of the considered geological settings, challenging recent findings by Aranda *et al.* (2013), who found no differences in SPARs among Macaronesian plant groups with varying dispersal ability.

I show that physical and bioclimatic island attributes, linked to environmental and dispersal filtering and speciation (Cavender-Bares *et al.* 2009; Kissling *et al.* 2012b), influence the phylogenetic structure and phylogenetic diversity of island floras (Chapter II.6). Environmental predictors explain more variation in phylogenetic diversity and structure for angiosperms and palms than for ferns, which is in accordance with expectations based on the high dispersal ability and large species ranges in ferns (Kessler 2010). When accounting for the effect of species richness on PD, PD is negatively related to isolation for palms but positively for angiosperms, indicating an influence of immigration from different biogeographic regions with distinct evolutionary histories to highly isolated islands. Island area has a negative effect on angiosperm and palm PD, indicating an effect of *in situ* speciation on large islands (Davies & Buckley 2011). However, phylogenetic clustering in angiosperm assemblages is also higher on large islands, indicating that on very large islands, which are mainly of continental origin, single radiations contribute little to overall *in situ* diversification relative to speciation events in distinct lineages.

The findings of this thesis are novel in a number of ways. I present the first environmental characterization of the world's islands (Weigelt *et al.* 2013a) (Chapter II.1). It quantitatively confirms some old yet unproven beliefs about contrasting mainland and island environments and provides novel insights into the environmental configuration and diversity of the world's islands (Fig. II.1.2). The combined framework of ordination and classification together with global environmental data (also compare Metzger *et al.* 2013) may open up new avenues for a more integrative use of islands in macroecological research. The predictions of vascular plant species richness that I provide for all 17,883 islands (Fig. II.1.5) are just one example of the variety of possible applications. Islands harbour a disproportionately high number of endemic species (Kier *et al.* 2009) and their biota are particularly threatened by biological invasions, habitat loss, and changing climate (Kier *et al.* 2009; Kueffer *et al.* 2010; Wetzel *et al.* 2013). The regionalization and data provided in Chapter II.1 (Weigelt *et al.* 2013b) may aid conservation prioritization.

I demonstrate that accurate data on physical island characteristics are needed to tackle such complex concepts as island isolation and intra-archipelagic spatial structure. Despite the long-appreciated importance of area and isolation for island species richness patterns (MacArthur & Wilson 1967), ecologically meaningful descriptors of island isolation and intra-archipelagic structure suitable for investigating, e.g., meta-population or source-sink dynamics on insular species richness or of intra-archipelagic migration on speciation and turnover have been lacking. Here, I present a suite of metrics filling this gap, as shown, e.g., by quantifying isolation in an island group as complex as the Southeast Asian archipelago. My results suggest that a variety of colonization and inter-island migration mechanisms influence plant diversity patterns on islands and archipelagos at macro-scales. The metrics developed should facilitate further research in island biogeography and could be applied in related fields like research on habitat fragmentation (see, e.g., Fahrig 2013).

The database of island plant species identities allows to analyze patterns and drivers of biodiversity beyond species richness (Kalmar & Currie 2006; Kreft *et al.* 2008). I provide the first analyses of α, β and γ diversity and phylogenetic diversity of insular systems at a global scale disentangling abiotic drivers and inferring processes. Together with functional diversity these components of global biodiversity have attracted increased research interest during the last years in macroecology (Beck *et al.* 2012), but some patterns like the latitudinal beta diversity gradient and the relationship between functional and phylogenetic diversity remain debated (Fritz & Purvis 2010; Kraft *et al.* 2011; Kraft *et al.* 2012; Qian *et al.* 2012; Tuomisto & Ruokolainen 2012). Islands may be key to answering some of the most compelling current macroecological questions and the species database presented here in combination with high resolution phylogenies and information on species traits will be supportive in this regard.

I show that relationships among environmental drivers and species richness as well as phylogenetic community attributes vary among taxonomic groups in dependence on their predominant dispersal- and speciation-related characteristics. This is a completely new perspective in island biogeography and allows inferences about underlying processes affecting island diversity, like dispersal and environmental filtering and speciation. Unlike in mainland systems (e.g. Davies & Buckley 2011), immigration and speciation on islands can directly be linked to measurable abiotic island characteristics like area and isolation. The results of this thesis thus help us to better understand the composition of plant assemblages in relation to plant physiological constraints and the abiotic environment in general, on mainlands as on islands. Understanding how the diversity of contrasting plant groups has originated from immigration and diversification may further help to elucidate how global diversity patterns came about. As shown here, islands may play a key role in achieving this goal.

Part IV

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Part V

Appendix

1. Supplementary information - Chapter II.1

Bioclimatic and physical characterization of the world's islands

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Text V.1.1. Material and Methods. We publish a data matrix of bioclimatic and physical characteristics, ordination and clustering results, and species richness predictions for the 17,883 islands > 1 km² investigated in this article as comma-separated text file (dx.doi.org/10.5061/dryad.fv94v, Weigelt *et al.* 2013b). The table is sorted by IDs (*ID*) unique to each island. Each island refers to a polygon in the GADM database of Global Administrative Areas, version 1 (www.gadm.org/version1/, Hijmans *et al.* 2009). Twelve islands identified in a previous study (Weigelt & Kreft 2013) to be missing from the GADM data or to be connected to continents erroneously (*IDs*: 85133, 85137, 85138, 85139, 85145, 85149, 85150, 100046, 100049, 100050) were drawn manually or clipped from continents. Longitude (*Long*) and Latitude (*Lat*) were calculated as polygon mass centroids. International Organization for Standardization country codes (*CountryISO*) and country names (*Country*) were adopted from GADM. In the case of multiple countries per island, country codes were amalgamated (up to 5 characters) and country names listed separated by semicolons. Where applicable, an archipelago name (*Archip*) was assigned.

For 11,546 islands, names (*Island*) were assigned using the NGA GEOnet Names Server (downloaded on March 29, 2012 from earth-info.nga.mil/gns/html/index.html; indicated as "gns" in column *Gazetteer*) for all regions but the United States, and the USGS Geographic Names Information System (downloaded on March 29, 2012 from geonames.usgs.gov/index.html; indicated as "gnis") for the United States. Only names classified as islands in these two resources were considered. Original ID (*Name_ID*) and geographic coordinates (*Name_long* and *Name_lat*) were adopted from the gazetteers. 7,475 islands were assigned single names that fell inside their polygons (indicated as "inside" in column *Name_meth*). In 1,751 cases, more than just one name was located inside an island polygon (*No_names*), e.g. due to erroneously located names of closely adjacent islands or inland freshwater islands. For all islands with ten or less names, the name located nearest (based on *Name_dist*; km) to the island's mass centroid was chosen automatically (indicated as "insideclosest"). In this case, the alternative names are also given (*Name_alt*). For 73 islands with more than ten names (large and well-known islands) the right name was chosen manually (indicated as "manually"). For 2,320 islands without a name within the polygon, names could be assigned because the island polygons were the closest features to island names not assigned previously and their mass centroids were not further than 10 km from the name's coordinates (indicated as "closest"). In this case, *No_names* indicates the number of names each polygon was the closest (based on *Name_dist*; km) feature for. If *No_names* was > 1, the closest name was chosen. A quality check of 100 randomly drawn islands for each method found that about 93% of the names of method "inside", 84% of method "insideclosest", and 78% of method "closest" can be assumed to be correct. Hence, the island names may help to find data for certain islands in our dataset but due to their insecure assignment they must not be used for automated match-ups. The island coordinates should be used instead as a spatially explicit reference.

Island area (*Area*; km^2) was calculated for each GADM polygon in cylindrical equal area projection. As measures of island isolation, we provide the distance from an islands mass centroid to the nearest mainland coast (*Dist*, km) measured in azimuthal equidistant projection using the 'Near Table' tool in ArcGIS Desktop 9.31 (ESRI, Redlands) and the $\log_{10}$-transformed sum of the proportions of landmass within buffer distances of 100, 1,000 and 10,000 km around the island perimeter (*SLMP*; Weigelt & Kreft 2013). Estimates of whether an island was connected to the mainland during the LGM or not (*GMMC*) were based on global bathymetry data (Amante & Eakins 2009) assuming a sea level decrease of -122 m at 18,000 years before present (Miller *et al.* 2005). However, this metric does not account for regional differences in sea level fluctuations and plate tectonics. Maximum elevation a.s.l. of each island (*Elev*; m) was extracted from the digital elevation model at 30 sec. resolution provided in WorldClim (Hijmans *et al.* 2005) which is based on SRTM (Jarvis *et al.* 2008) and GTOPO30 (USGS 1996) using the 'Zonal Statistics' tool in ArcGIS. For 1,891 small islands that did not fully enclose a 30 sec. WorldClim raster cell, we applied a 1 km buffer as indicated in column *Buffer*.

We extracted bioclimatic variables from WorldClim (BIO1, BIO7, BIO12, and BIO15) in a similar manner to *Elev*. When interpreting the climate patterns one has to consider possible shortcomings of the WorldClim data. WorldClim interpolates climatic measurements between climate stations accounting for latitude, longitude, and elevation but disregards other important information like slope aspect or predominant wind directions (Hijmans *et al.* 2005). Especially for precipitation in mountainous tropical regions with few climate stations, the data might be imprecise (Soria-Auza *et al.* 2010).

Here, we provide maximum values per island polygon of annual mean temperature (*Temp*; °C) and annual precipitation (*Prec*; mm) and minimum values of the annual temperature range (*varT*; °C) and the coefficient of variation in monthly precipitation (*varP*). For a region of 129 islands > 1 km^2 including parts of French Polynesia and the Pitcairn islands that lack WorldClim temperature data, we modelled *Temp* and *varT* based on the relationships of sea surface temperature and its range with *Temp* and *varT* on neighbouring islands. We extracted sea surface temperature data (Reynolds *et al.* 2002) for all islands of French Polynesia, the Cook Islands, The Pitcairn islands, Kiribati, Wallis and Futuna, Fiji, American Samoa, Niue, Tokelau, Tonga, and Samoa. We then fitted linear models of the maximum values of annual mean temperature and minimum values of the temperature range from WorldClim for the islands covered by WorldClim (n = 255) and mean annual sea surface temperature (*ssTemp*) and range (*ssvarT*) and used the model to predict maximum mean annual temperature and minimum temperature range for the islands not covered ($Temp = -9.36 + 1.29 \times ssTemp$, $R^2 = 0.87$, $P < 0.001$; $varT = 4.96 + 1.39 \times ssvarT$, $R^2 = 0.93$, $P < 0.001$). Islands with modelled temperature data are marked in column *modeled_T*.

We calculated climate change velocity (*CCVT*; in meters per year) since the LGM 21,000 years ago following Loarie *et al.* (2009) and Sandel *et al.* (2011). Climate change velocity is the ratio between the temporal change in temperature (temporal gradient) and the contemporary spatial change in temperature (spatial gradient), and is expressed in distance units per time. We calculated the temporal gradient as the difference between the current annual mean temperature and the annual mean temperature at the LGM divided by 21,000 years. Current climate data were based on the 30 sec. WorldClim data and our model predictions for parts of French Polynesia and the Pitcairn islands. Based on the predicted maximum annual mean temperature at sea level as intercepts, we modelled annual mean temperatures (*meanT*) for each WorldClim raster cell of the 129 missing islands. We used the mean slope of regressions between WorldClim annual mean temperature and elevation a.s.l. for the neighbouring highly elevated volcanic islands Tahiti, Raiatea, Savaii, Upolu, and Kauai ($meanT = Temp + (-0.0056) \times Elevation$; R^2 values of all $meanT \sim Elevation$ models > 0.99, all p-values < 0.001). Data from two past climate models (CCSM3 and MIROC3.2) were taken from the Paleoclimate Modeling Intercomparison Project Phase II (Braconnot *et al.* 2007). We used the mean of the two model predictions as LGM mean annual temperature according to Sandel *et al.* (2011). For comparison with current climate, we down-scaled the estimates to 30 sec. resolution and then calculated the spatial mean annual temperature gradient based on the contemporary climate data as the slope from each raster cell to its four nearest neighbours. To avoid dividing by zero, all values below 0.01 °C/km and values of cells with less than four direct neighbours were replaced with 0.01 °C/km. We then extracted mean values of climate change velocity for each island. If not stated otherwise above, GIS analyses were performed using R statistical software version 2.14.2

(R Development Core Team 2010) and packages *sp* (Pebesma *et al.* 2012), *maptools* (Bivand *et al.* 2013b), raster (Hijmans & van Etten 2012) and *rgdal* (Bivand *et al.* 2013a).

Column names starting with "*PAM*" refer to results from non-hierarchical partitioning around medoids (PAM), and column names starting with "*UPGMA*" refer to results from the hierarchical unweighted pair-group method with arithmetic mean (UPGMA). Axis scores of principal component analyses (PCA) are stored in columns starting with "*PCA*". Name suffixes refer to the set of bioclimatic and physical variables considered in each case (*nAE* = all variables except *Area* and *Elev*; *all* = all ten variables; *cli* = contemporary bioclimatic variables; *geo* = physical variables). For all combinations of clustering method and variable subset we present eight distinct groups. We used the Caliński and Harabasz index (Caliński & Harabasz 1974) to determine the optimal number of clusters. In the majority of cases for UPGMA, the optimum or local optimum was reached at eight clusters. However, for PAM, index values usually decreased with increasing number of clusters. We therefore adopted the number of eight clusters for all presented regionalizations since eight clusters were well suited for graphical presentation and conceptual discussion. This semi-quantitative approach is in line with other studies that highlight the adequacy of choosing an arbitrary number of clusters (Metzger *et al.* 2013). Ordination, cluster analyses and evaluation were performed using the R-packages *vegan* (Oksanen *et al.* 2013), *flashClust* (Murtagh *et al.* 2012), *cluster* (Maechler 2012), and *fpc* (Hennig 2013).

As demonstration application of the presented data and multivariate framework in macroecology and biogeography, we used it to develop statistical predictions of the species richness of native vascular plants on all 17,883 islands > 1 km². We built on existing richness data for vascular plants, including all 345 islands from Weigelt and Kreft (2013) that could be assigned to a single GADM polygon (Sachet 1962; Ferro & Furnari 1968; Johnson *et al.* 1968; Ferro & Furnari 1970; Simberloff 1970; Young 1971; Johnson & Simberloff 1974; Renvoize 1975; Abbott 1978; Cronk 1980; Hansen 1980; Sykes 1981; Buckley 1983; Case & Cody 1983; Whistler 1983; Wright 1983; Druce 1984; Davis *et al.* 1986; Rannie 1986; Lawesson *et al.* 1987; Bocchieri 1988; Levin & Moran 1989; Brodie & Sheehy Skeffington 1990; Borhidi 1991; Hoffmann & Teillier 1991; Snogerup *et al.* 1991; Bocchieri 1992; Groombridge 1992; Thaman 1992; Hnatiuk 1993; Turland *et al.* 1993; Borkowsky 1994; Davis *et al.* 1994; de Leonardis & Zizza 1994; Harvey 1994; Malyshev 1994; Sosa & Dávila 1994; Brullo *et al.* 1995; d'Antonio & Dudley 1995; Davis *et al.* 1995; Florence *et al.* 1995; Gamisans & Jeanmonod 1995; Jahn & Schönfelder 1995; MacDonald & Cooper 1995; Batianoff & Dillewaard 1996; Christodoulakis 1996; Lowry II 1996; Cronk 1997; Davis *et al.* 1997; Florence & Lorence 1997; Gabrielsen *et al.* 1997; Médail & Quézel 1997; Medail & Verlaque 1997; Baldini 1998; Chown *et al.* 1998; Médail & Vidal 1998; Stuessy *et al.* 1998; Sun & Stuessy 1998; Zanoni & Buck 1999; Baldini

2000; Barkalov 2000; Hobohm 2000; Moody 2000; Baldini 2001; Frodin 2001; Panitsa & Tzanoudakis 2001; Lawesson & Skov 2002; Pietsch *et al.* 2003; Dahl 2004; Meyer 2004; Price 2004; Roos *et al.* 2004; McMaster 2005) and 130 islands for which data was available from published floras, checklists and online databases (Marquand 1901; Lester-Garland 1903; Egorova 1964; D'Arcy 1971; Greene & Walton 1975; Esler 1978; Proctor 1980; Byrd 1984; Hill 1986; Kamari *et al.* 1988; Dowhan & Rozsa 1989; Burton 1991; Du Puy 1993; Moran 1996; Sandbakk *et al.* 1996; Junak *et al.* 1997; Whistler 1998; Butler *et al.* 1999; de Lange & Cameron 1999; Convey *et al.* 2000; Brofas *et al.* 2001; Case *et al.* 2002; Christmas Island National Park 2002; Hill 2002; Takahashi *et al.* 2002; Gerlach 2003; McCrea 2003; Robinson *et al.* 2003; Arechavaleta *et al.* 2005; Wagner *et al.* 2005; Gage *et al.* 2006; Kelly 2006; Raulerson 2006; Searle & Madden 2006; Stalter & Lamont 2006; Takahashi *et al.* 2006; Florence *et al.* 2007; UIB 2007; Franklin *et al.* 2008; Robinson *et al.* 2008; Wellington Botanical Society 2008; CARMABI 2009; Shaw *et al.* 2010; Jaramillo Díaz & Guézou 2011; University of Kent 2012). Following the rational of (Kreft *et al.* 2008) we used as predictors the ten bioclimatic and physical variables presented here. As additional predictor we included the species richness of the closest mainland grid cell derived from the co-kriging based estimates provided by Kreft and Jetz (2007) (column *SRML*). We allowed for first order interactions among *Area* and *Temp*, *Dist* and *SRML*, *Temp* and *Prec*, as well as *Area* and *Dist*. For comparison, we fitted generalized linear models (GLMs) of the Gaussian and Poisson families, spatial simultaneous autoregressive lag models (SARs) accounting for spatial autocorrelation (Bivand *et al.* 2011), and generalized additive models (GAMs) allowing non-linear and spatial effects (Wood 2003; Wood 2006). We preferred SARs of the lag type over SARs of the error type since the latter does not consider the spatial effect in predictions for new data (Bivand *et al.* 2011). In GLMs and SARs all variables were included as linear effects. For both, based on corrected Akaike information criterion (AIC_c)-based model comparisons and to reduce skewness, we $\log_{10}$-transformed the following predictors: *Area*, *SLMP* + 0.5, *Elev* + 1, *CCVT* + 1, *Prec* +1, and *SRML* (constants were added to avoid taking the logarithm of zero). Optimal lag distances for SARs were defined following Kissling and Carl (2008) evaluating model AICs and the improvement of Moran's I values of spatial autocorrelation in model residuals compared to non-spatial GLMs. In GAMs, each factor was added as penalized regression splines with up to three degrees of freedom (Wood 2003; Wood 2006). Interactions were added as tensor product interactions with up to three degrees of freedom for each basis. In addition to the aforementioned interactions, GAMs included an isotropic smooth of *Lat* and *Long* on a sphere to account for spatial patterns in the response variable. All variables entered the GAMs untransformed except *Area* which was $\log_{10}$-transformed after visual model inspection. For all model types, we ran a model selection procedure to identify the best among all possible candidate models and conducted multi-model inference by averaging all candidate models up to a sum of AIC$_c$-weights of 0.95 (Burnham & Anderson 2002). Although smooth terms in GAMs are already penalized to prevent overfitting, the minimum degrees of freedom is larger than zero (Wood & Augustin 2002) necessitating further model selection. Despite the “count” nature of the response variable, Gaussian GLMs with log$_{10}$-transformed species richness as response variable performed better than Poisson GLMs of untransformed richness in terms of model fit and model diagnostics (pseudo R^2 of best Poisson candidate model = 0.671 compared to pseudo R^2 of best Gaussian candidate model = 0.734). Furthermore, the use of SARs did not improve model fit compared to GLMs (pseudo R^2 of best SAR candidate model = 0.705). We therefore do not present results and predictions from Poisson GLMs and SARs. Model statistics and predictions from the best candidate models were very similar to those based on multi-model inference (e.g. pseudo R^2 of best Gaussian GLM and pseudo R^2 of averaged Gaussian GLMs both = 0.734; pseudo R^2 of best GAM = 0.937 compared to pseudo R^2 of averaged GAMs = 0.936). However, we focus on predictions from multi-model inference here because for both GLMs and GAMs their prediction error (averaged mean error based on 10-fold cross validation) was slightly smaller (GLM: best model prediction error = 0.137, averaged model prediction error = 0.127; GAM: best model prediction error = 0.044, averaged model prediction error = 0.031). Predicted species numbers together with their standard errors can be found in the columns *SR_GLM* and *SR_SE_GLM* for GLM predictions and *SR_GAM* and *SR_SE_GAM* for GAM predictions. Both species richness and standard errors were back-transformed (as log$_{10}$ (species richness + 1) was the modelled response variable) to represent actual species numbers. In the main results (Figs. II.1.4 & II.1.5), we focus on predictions based on GAMs because they are more flexible, account for spatial patterns, fit the data better (AIC best GAM = -167.8, AIC best GLM = 392.6), and yield more realistic predictions in regions where the other approaches strongly overestimate richness (e.g. on the western coasts of Africa and Canada; Fig. V.1.7). Model averaging and multi-model inference, generalized additive models, spatial simultaneous autoregressive models and k-fold cross validation were applied using the R-packages *MuMIn* (Barton 2013), *mgcv* (Wood 2003; Wood 2006), *spdep* (Bivand *et al.* 2011), and *boot* (Canty & Ripley 2012).

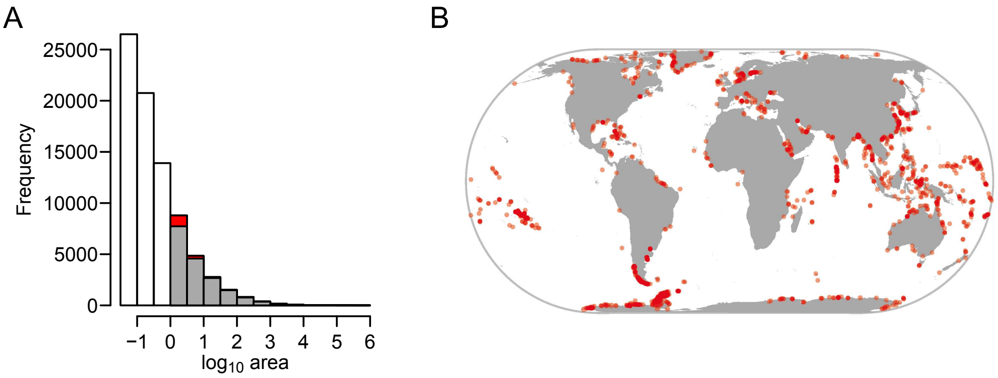

Figure V.1.1. (A) Histogram of area size of all 80,604 islands > $10^{-1.5}$ km² included in the GADM dataset (Hijmans *et al.* 2009). The 17,883 > 1 km² islands considered in the bioclimatic and physical characterization are shown in grey. 1,509 islands > 1 km² that were not included due to lacking climate data are collared red and mapped in (B). These encompass mainly islands only slightly larger than 1 km² distributed more or less evenly across island rich regions of the globe, and include also all islands south of -60°, where no WorldClim climate data coverage is available (Hijmans *et al.* 2005).

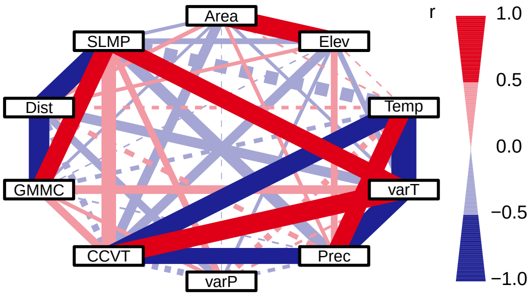

Figure V.1.2. Correlations among bioclimatic and physical variables for 17,883 islands > 1 km² worldwide. Coefficients and p-values were corrected for spatial autocorrelation. Solid lines denote significant relationships at P < 0.05, whereas dashed lines are non-significant. Abbreviations follow Text V.1.1.

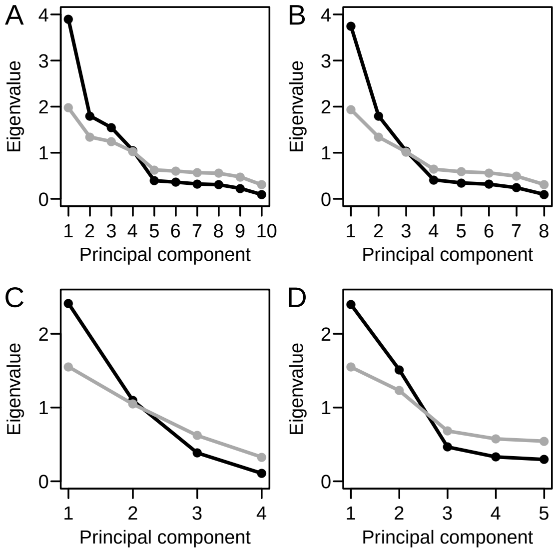

Figure V.1.3. Scree plots of eigenvalues (black) of principal components. PCAs were conducted for 17,883 islands > 1 km² worldwide including (A) all ten bioclimatic and physical variables used in the bioclimatic and physical characterization of the world's islands, (B) all variables but *Area* and *Elev*, (C) contemporary bioclimatic variables only (*Temp*, *varT*, *Prec*, *varP*), and (D) physical variables only (*Area*, *Elev*, *Dist*, *SLMP*, *GMMC*). Abbreviations follow Text V.1.1. Grey dots and lines indicate square roots of eigenvalues used for weighting in cluster analyses.

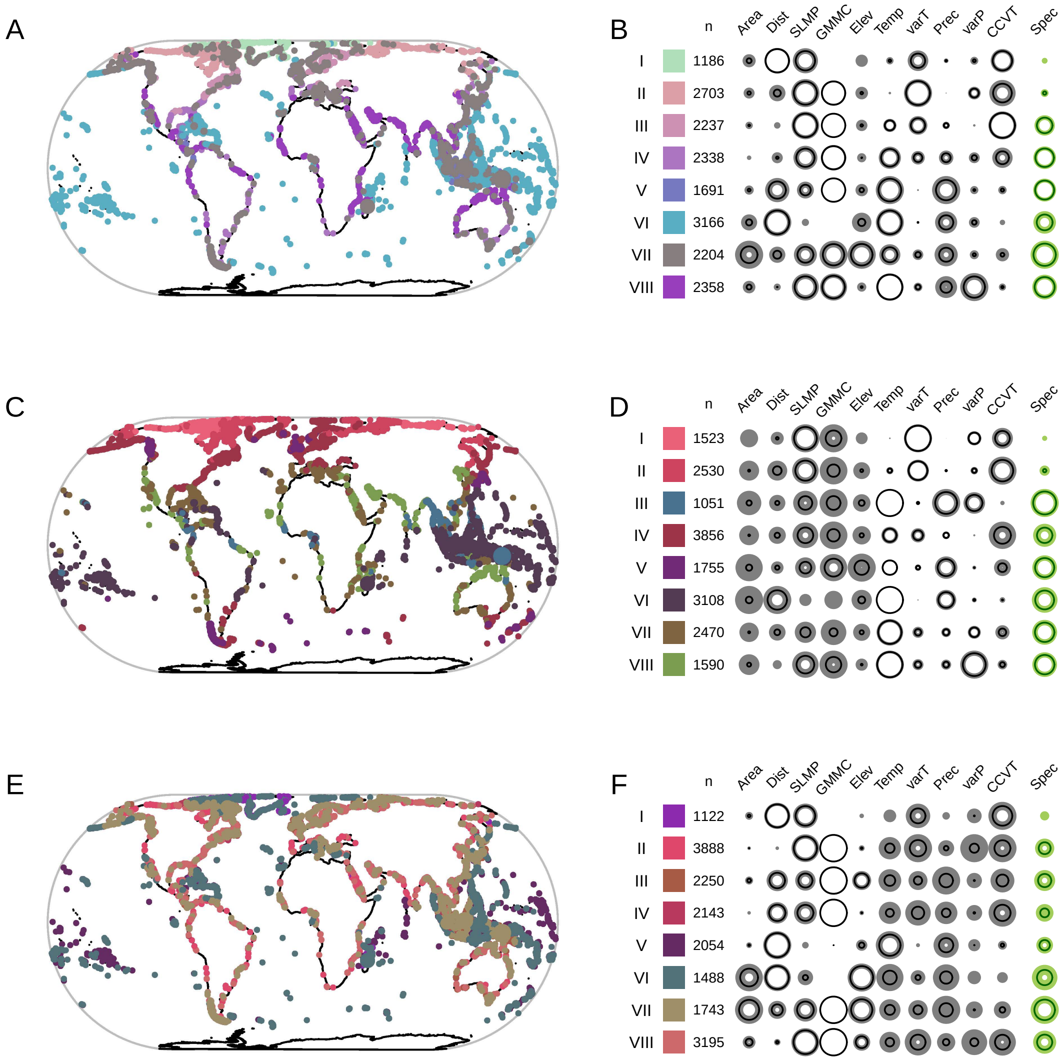

Figure V.1.4. PAM clustering using weighted PCA axes (Euclidean distance) based on (A-B) all ten variables, (C-D) contemporary bioclimatic variables only (*Temp*, *varT*, *Prec*, *varP*), and (E-F) physical variables only (*Area*, *Dist*, *SLMP*, *GMMC*, *Elev*). Colours were calculated as mean RGB values of all constituent islands of each cluster based on the corresponding PCA colours in Fig. II.1.2. Points were plotted in decreasing order of *Area*. Circles in B, D, and F indicate variable characteristics within clusters: Circle = arithmetic mean; shaded ring = standard deviation. Abbreviations follow Text V.1.1. *Spec* indicates predicted vascular plant species richness.

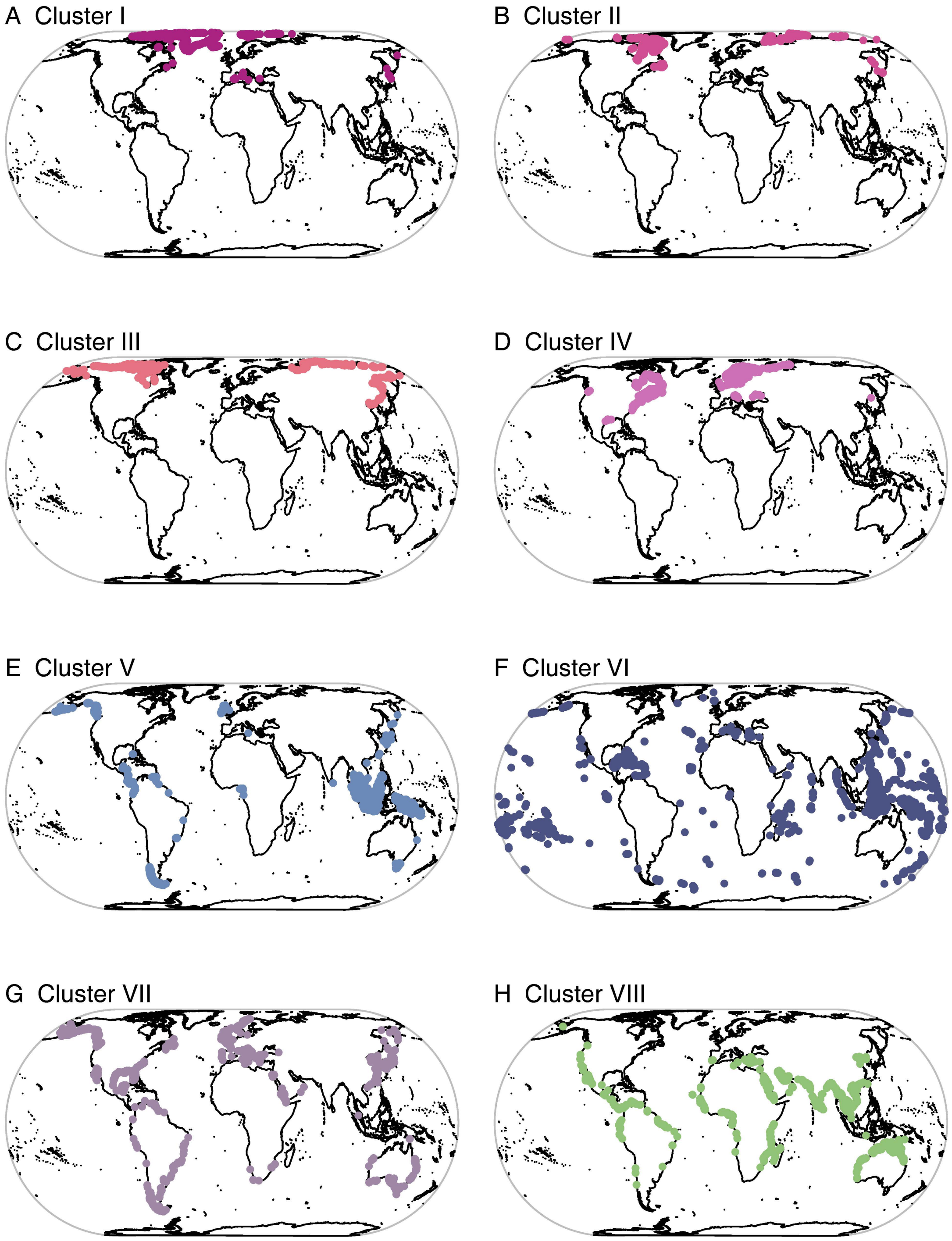

Figure V.1.5. Ecoregions derived from PAM clustering using weighted PCA axes (Euclidean distance) calculated for 17,883 islands > 1 km² worldwide. Each map in A-H refers to one cluster (I-VIII) in Fig. II.1.4. PCA was based on eight environmental variables (*Dist*, *SLMP*, *GMMC*, *Temp*, *varT*, *CCVT*, *Prec*, *varP*), excluding *Area* and *Elev*. Abbreviations follow Text V.1.1. Colours are calculated as mean RGB values of all constituent islands of each cluster based on the PCA colours in Fig. II.1.2E.

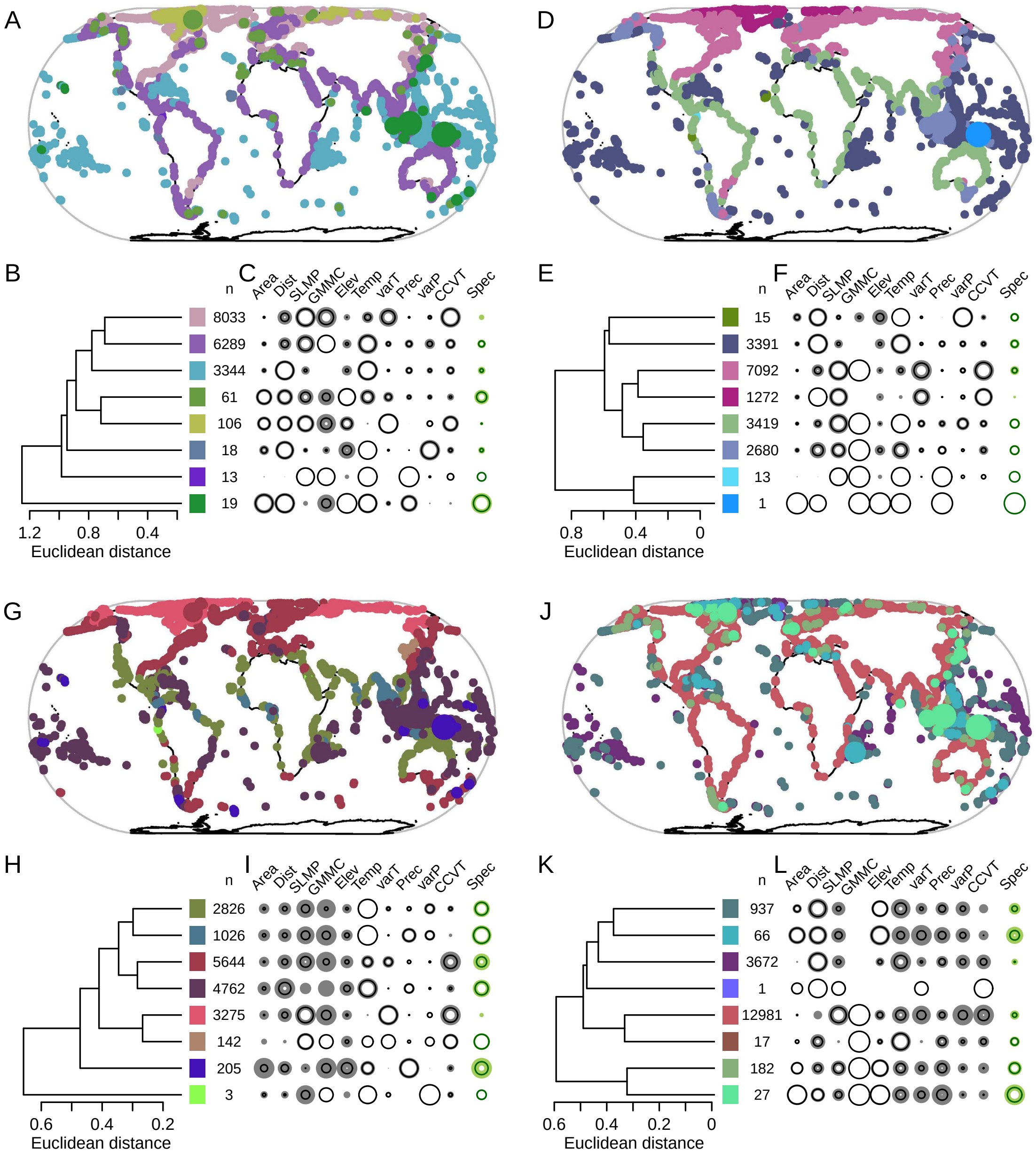

Figure V.1.6. UPGMA clustering using weighted PCA axes (Euclidean distance) based on (A-C) all ten variables, (D-F) all variables but *Area* and *Elev*, (G-I) contemporary bioclimatic variables only (*Temp*, *varT*, *Prec*, *varP*), and (J-L) physical variables only (*Area*, *Dist*, *SLMP*, *GMMC*, *Elev*). Colours were calculated as mean RGB values of all constituent islands of each cluster based on the corresponding PCA colours in Fig. II.1.2. Points were plotted in decreasing order of *Area*. Circles in C, F, I, and L indicate variable characteristics within clusters: Circle = arithmetic mean; shaded ring = standard deviation. Abbreviations follow Text V.1.1. *Spec* indicates predicted vascular plant species richness.

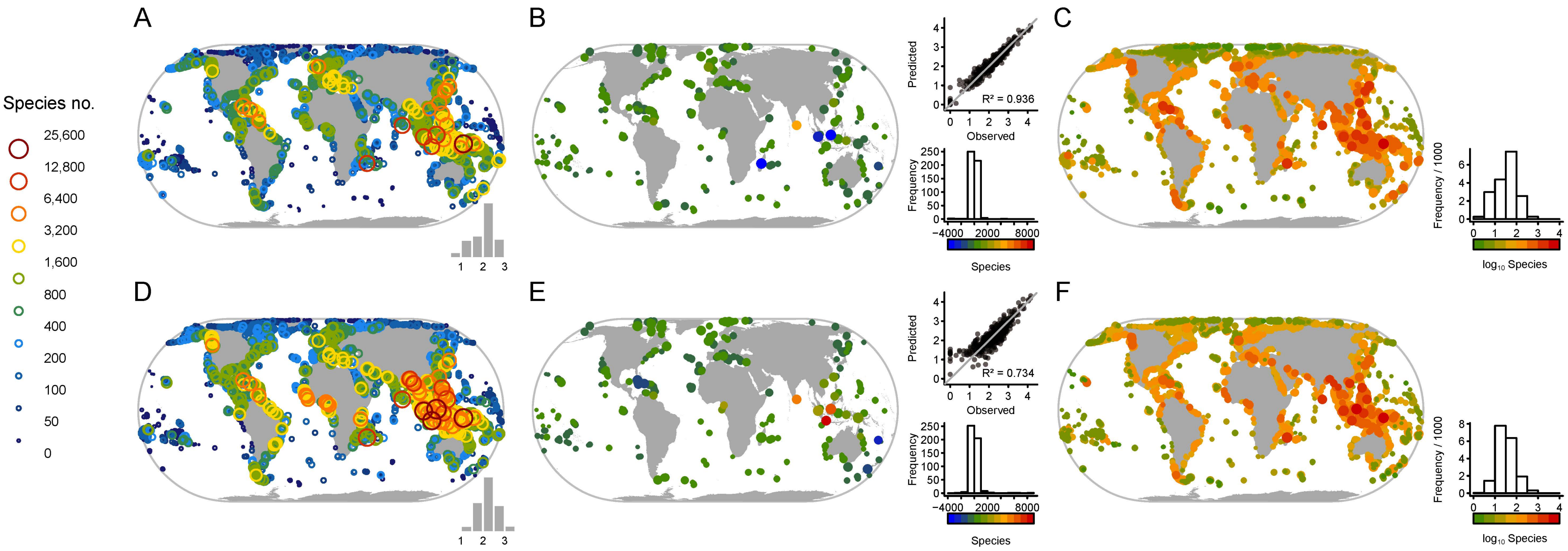

Figure V.1.7. Predicted pattern of species richness for vascular plants on 17,883 islands > 1 km² worldwide based on model averaging of generalized additive models (A - C), and generalized linear models (D - F). A and D show the predicted species richness values (with circles plotted in order of increasing species richness and embedded histograms providing an impression of the distribution of predicted richness on a logarithmic scale ($\log_{10}$ (species richness + 1)). B and E show residual species richness for the islands included in the training dataset (side plots provide bi-plots of observed vs. predicted values and corresponding pseudo R^2-values). C and F show standard errors of the richness predictions. In B, C, E and F values are plotted in order of decreasing frequency to show rare values on top of frequent values if points overlap. Both residuals and standard errors were back-transformed (as $\log_{10}$ (species richness + 1) was the modelled response variable) to represent actual species numbers.

Table V.1.1. Summary statistics of ten bioclimatic and physical variables for 17,883 islands > 1 km² worldwide (untransformed). Abbreviations follow Text V.1.1. All Moran's I values are significant at *P* < 0.001 except for area (*P* = 0.433).

	Area	*Dist*	*SLMP*	*GMMC*	*Elev*	*Temp*	*varT*	*Prec*	*varP*	*CCVT*
Min	1.00	0.00	0.12	0.00	0.00	-210.00	53.00	0.00	0.00	0.00
Mean	428.99	441.64	1.11	0.74	98.24	113.56	229.98	1446.61	46.77	35.71
Median	4.08	50.84	1.17	1.00	13.00	111.00	196.00	1191.00	40.00	15.71
Max	773633.97	6067.08	2.17	1.00	4613.00	314.00	613.00	7628.00	193.00	168.57
SD	11372.76	811.98	0.41	0.44	251.19	146.57	127.35	1152.59	29.26	37.68
Moran's I	0.00	0.94	0.70	0.58	0.10	0.99	0.92	0.75	0.78	0.82
Unit	km²	km	-	YES/NO	m	°C * 10	°C * 10	mm	-	m/a

Table V.1.2. Matrix of Pearson correlation coefficients among ten bioclimatic and physical variables for 17,883 islands > 1 km². Correlations with geologic age could only be calculated for a subset of 102 volcanic islands. A correlation coefficient between island age and GMMC is not given because age was only assessed for islands not connected to the mainland during the last glacial maximum. Correlation coefficients and significances were corrected for spatial autocorrelation: *** (*P* < 0.001), ** (*P* < 0.01), * (*P* < 0.05). Abbreviations follow Text V.1.1.

	Area	*Elev*	*Temp*	*varT*	*Prec*	*varP*	*CCVT*	*GMMC*	*Dist*	*SLMP*
Elev	0.618***									
Temp	0.064	0.048								
varT	-0.111**	-0.182*	-0.835**							
Prec	0.126***	0.226***	0.583*	-0.692**						
varP	-0.027	-0.119**	0.219	0.090	-0.126					
CCVT	-0.326***	-0.312***	-0.633*	0.635*	-0.533*	-0.216				
GMMC	-0.101***	-0.048	-0.150	0.288**	-0.059	0.131*	0.264**			
Dist	0.141***	0.126**	0.120	-0.334*	0.170	-0.259**	-0.230	-0.685***		
SLMP	-0.115***	-0.191***	-0.431	0.590**	-0.393*	0.225*	0.486*	0.583***	-0.658***	
Age	0.049	-0.248*	0.195*	-0.209*	-0.182	0.203*	0.140	-	-0.416***	0.381***

Table V.1.3. Axis scores of variables used in PCAs calculated for 17,883 islands > 1 km² worldwide and axis eigenvalues, based on (A) all ten bioclimatic and physical variables, (B) all variables but *Area* and *Elev*, (C) contemporary bioclimatic variables only, and (D) physical variables only. Abbreviations follow Text V.1.1.

A	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**
Area	-0.165	0.014	-0.664	0.160	-0.598	0.205	-0.021	0.239	0.211	0.062
Elev	-0.185	0.013	-0.660	-0.059	0.501	-0.351	-0.232	-0.288	-0.087	-0.087
Temp	-0.374	-0.372	0.211	0.027	-0.315	-0.330	-0.251	-0.014	-0.018	-0.636
varT	0.441	0.177	-0.152	0.187	0.207	0.245	0.207	0.089	0.195	-0.724
Prec	-0.354	-0.247	0.025	-0.416	0.224	0.675	-0.128	-0.155	0.298	-0.072
varP	0.051	-0.423	0.072	0.744	0.261	0.134	-0.314	0.060	0.184	0.192
GMMC	0.268	-0.458	-0.142	-0.361	0.168	-0.066	-0.085	0.699	-0.199	0.022
Dist	-0.294	0.498	0.084	0.150	0.109	0.284	-0.417	0.350	-0.484	-0.115
SLMP	0.403	-0.265	-0.125	-0.021	-0.266	0.302	-0.201	-0.461	-0.579	-0.042
CCVT	0.394	0.248	0.083	-0.234	-0.139	-0.129	-0.710	-0.039	0.423	0.046
Eigenvalue	3.895	1.800	1.547	1.050	0.395	0.363	0.323	0.307	0.227	0.093

B	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Temp	-0.397	0.368	-0.044	0.546	-0.032	-0.006	0.096	0.630
varT	0.460	-0.174	-0.176	-0.373	0.018	-0.053	-0.214	0.735
Prec	-0.362	0.246	0.420	-0.403	0.580	0.156	-0.318	0.085
varP	0.046	0.422	-0.762	-0.031	0.363	-0.186	-0.175	-0.200
GMMC	0.282	0.461	0.372	-0.118	-0.037	-0.697	0.263	-0.011
Dist	-0.303	-0.500	-0.153	-0.098	0.443	-0.335	0.552	0.110
SLMP	0.418	0.268	0.036	0.019	0.299	0.566	0.585	0.024
CCVT	0.390	-0.249	0.215	0.613	0.493	-0.139	-0.313	-0.054
Eigenvalue	3.748	1.800	1.037	0.413	0.346	0.318	0.242	0.097

C	**PC1**	**PC2**	**PC3**	**PC4**
Temp	-0.583	0.261	-0.391	-0.663
varT	0.608	0.076	0.347	-0.710
Prec	-0.539	-0.202	0.813	-0.085
varP	-0.003	0.941	0.255	0.223
Eigenvalue	2.412	1.095	0.385	0.108

D	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Area	-0.250	0.657	0.477	0.519	-0.098
Elev	-0.252	0.661	-0.400	-0.578	0.074
GMMC	0.524	0.257	-0.483	0.459	0.465
Dist	-0.558	-0.202	0.099	0.046	0.798
SLMP	0.537	0.156	0.608	-0.430	0.364
Eigenvalue	2.397	1.512	0.465	0.330	0.295

Table V.1.4. Summary statistics for clusters from PAM clustering using weighted PCA axes (Euclidean distance) based on (A) all ten bioclimatic and physical variables, (B) all variables but *Area* and *Elev*, (C) contemporary bioclimatic variables only (*Temp*, *varT*, *Prec*, *varP*), and (D) physical variables only (*Area*, *Elev*, *Dist*, *SLMP*, *GMMC*). Abbreviations follow Text V.1.1. *Spec* indicates predicted vascular plant species richness. Note that cluster numbers in A to D do not correspond to each other but refer to Fig. II.1.4 and Fig. V.1.5 for B and to Fig. V.1.4 for A, C and D.

A	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
Area	41±217	44±419	8±17	4±11	11±28	124±779	3181±3225	24±81
Dist	1047±328	132±176	27±73	73±162	546±473	1486±1314	161±297	35±130
SLMP	1.23±0.27	1.42±0.27	1.44±0.22	1.18±0.26	0.86±0.24	0.51±0.2	1.08±0.3	1.33±0.27
GMM	0±0	0.99±0.08	1±0	0.99±0.09	1±0	0±0	0.91±0.29	0.96±0.19
Elev	65±139	40±81	28±49	20±35	34±56	145±319	404±466	22±43
Temp	-7.5±7.2	-11.2±3.8	3.8±4.5	14.8±6.8	22.5±8	23.8±6.4	11±8.9	25.9±3.5
varT	30.7±8.9	44.3±5.9	30.6±6.3	22.6±7	10.4±2.6	11.1±3.4	18.2±7.2	17.3±5.5
Prec	446±398	260±128	830±354	1374±677	2791±965	2036±973	2003±1138	1692±1290
varP	34.3±18	55.8±13.2	24.4±8.7	42.7±19.7	31.3±21.6	40.3±21.6	34.9±21	98.8±23.9
CCVT	57.3±21.12	62.61±38.8	97.55±27.3	34.63±23.6	11.13±7.27	7.73±3.89	16.27±16.9	9.76±4.54
Spec	18±26	25±29	147±107	212±120	231±168	188±231	469±690	287±227

B	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
Area	438±6197	649±14247	199±5775	30±302	1334±2415	656±11894	90±2306	37±174
Dist	1036±335	256±183	34±77	17±48	418±462	1445±1309	86±177	23±81
SLMP	1.23±0.27	1.23±0.2	1.55±0.23	1.44±0.22	0.88±0.25	0.52±0.22	1.16±0.28	1.35±0.26
GMM	0±0	1±0	1±0.04	1±0	1±0	0±0	0.99±0.1	0.97±0.17
Elev	113±259	67±151	29±65	38±89	162±346	175±392	98±181	37±96
Temp	-7.3±7.4	-8.4±5	-11.9±5	3.6±4.9	20±9.2	23.6±6.6	13.8±7	25.9±3.1
varT	30.6±9	39±4.7	47.8±4.8	30.7±6.7	11.1±2.9	11.3±3.7	21.5±6.4	17.3±5.5
Prec	468±418	382±243	225±153	834±382	2855±971	2011±994	1428±702	1730±1277
varP	33.9±18.1	45.8±13.3	62.8±13.9	25.2±9.1	31.3±22.3	41.1±22.6	40.6±18.1	98.8±23.7
CCVT	54.44±22.7	87.35±32.1	35.71±21.5	97.01±29.1	9.33±5.47	7.65±3.94	29.75±21.3	9.57±4.59
Spec	23±39	31±39	35±51	151±129	334±550	216±378	261±189	314±260

C	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
Area	321±5939	431±11207	823±23872	169±2743	711±9603	995±19228	72±778	36±187
Dist	144±251	364±467	310±546	325±602	161±454	1323±1298	251±516	105±291
SLMP	1.47±0.24	1.36±0.28	1.12±0.39	1.19±0.37	1.03±0.31	0.68±0.35	0.99±0.37	1.27±0.34
GMM	0.87±0.34	0.78±0.41	0.82±0.39	0.78±0.41	0.93±0.26	0.44±0.5	0.67±0.47	0.86±0.34
Elev	35±79	75±180	81±253	95±232	219±324	130±353	83±222	42±130
Temp	-14.2±2.5	-7.5±4.6	26.7±0.8	6.4±5.8	8.2±2.7	26.6±1.1	21.9±5.2	25±4.4
varT	48.2±4	38.1±4.7	12.5±3.5	24.5±6.6	15.3±3.9	9.3±1.9	19.3±6.9	19.3±6.8
Prec	159±64	377±172	3508±957	978±360	2754±849	2559±696	1112±527	1057±648
varP	66.2±10	40.1±11.3	83.9±20	23.2±7.9	25.2±12.8	29.8±11.7	59.4±12.4	108.6±19.7
CCVT	38.86±22.7	79.63±35.5	6.54±3.13	61.72±41.8	24.73±25.9	7.46±3.45	18.97±16.3	12.3±8.79
Spec	19±20	36±41	411±506	177±178	247±279	294±519	254±210	254±207

D	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
Area	9±42	3±4	7±7	3±4	5±6	1817±1854	2787±3202	17±26
Dist	978±403	5±7	316±359	332±365	1575±1437	1191±946	179±296	11±17
SLMP	1.22±0.24	1.41±0.25	0.98±0.26	1.07±0.3	0.49±0.18	0.68±0.36	1.1±0.3	1.43±0.24
GMM	0±0	1±0	1±0.06	1±0	0±0.02	0±0	1±0.02	1±0.04
Elev	5±15	5±5	80±82	4±4	17±26	466±512	369±410	54±71
Temp	-0.4±14.3	10.2±14.5	11.7±13.4	8.6±15.9	23.5±7.6	15.1±15.1	10.9±12.6	9.2±13.7
varT	27.1±10.2	28.7±12.5	20.1±11.4	24.5±13.9	11.3±4.2	16.7±10.3	20.9±11.1	27.3±12.2
Prec	676±656	1074±991	1858±1250	1428±1201	1915±953	1749±1222	1842±1275	1237±1024
varP	41.3±24.9	56.1±34	41.6±25.6	42.5±25.4	40±21.4	39.6±24.1	42±28	54.1±31.8
CCVT	50.61±25.4	48.21±43.1	34.94±36.0	47.91±42.1	10.89±12.9	11.4±15.28	19.36±22.1	43.79±40.1
Spec	43±65	144±112	177±136	110±92	102±61	335±536	512±675	241±205

Table V.1.5. Variable importance of all ten bioclimatic and physical variables, mainland plant species richness and interaction terms for vascular plant species richness on 475 islands > 1 km² worldwide. Variable importance was assessed as cumulative AIC_c-weights based on multi-model inference for generalized additive models (GAM) and generalized linear models (GLM). In addition to the here listed variables, all candidate GAMs included an isotropic smooth of *Lat* and *Long* on a sphere to account for spatial patterns. Abbreviations follow Text V.1.1.

	GAM	**GLM**
Area	1.00	1.00
Dist	0.83	1.00
SLMP	1.00	1.00
GMMC	0.74	0.39
Elev	0.56	0.30
Temp	1.00	1.00
varT	0.30	0.26
CCVT	0.31	0.39
Prec	1.00	1.00
varP	0.27	0.27
SRML	0.33	1.00
Area:Temp	0.97	0.96
Prec:Temp	0.29	0.87
Dist:Area	0.70	0.67
Dist:SRML	0.13	1.00

2. Supplementary information - Chapter II.2

Quantifying island isolation – insights from global patterns of insular plant species richness

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Text V.2.1. The following references were used to compile the dataset of vascular plant species richness on 453 islands worldwide for Chapter II.2: Fosberg 1937; St John 1948; Glassman 1953; Sachet 1962; Ferro & Furnari 1968; Johnson *et al.* 1968; Ferro & Furnari 1970; Simberloff 1970; Parham 1971; Young 1971; Johnson & Simberloff 1974; Renvoize 1975; Abbott 1978; Cronk 1980; Hansen 1980; Sykes 1981; Buckley 1983; Case & Cody 1983; Whistler 1983; Wright 1983; Druce 1984; Wester 1985; Davis *et al.* 1986; Rannie 1986; Lawesson *et al.* 1987; Bocchieri 1988; Major 1988; Carlson & Clemendson 1989; Levin & Moran 1989; Thomas *et al.* 1989; Brodie & Sheehy Skeffington 1990; Borhidi 1991; Hoffmann & Teillier 1991; Snogerup *et al.* 1991; Bocchieri 1992; Groombridge 1992; Thaman 1992; Hnatiuk 1993; Telford 1993; Turland *et al.* 1993; Borkowsky 1994; Davis *et al.* 1994; de Leonardis & Zizza 1994; Green 1994b; Harvey 1994; Malyshev 1994; Sosa & Dávila 1994; Williams 1994; Bocchieri 1995; Brullo *et al.* 1995; d'Antonio & Dudley 1995; Davis *et al.* 1995; Florence *et al.* 1995; Gamisans & Jeanmonod 1995; Jahn & Schönfelder 1995; MacDonald & Cooper 1995; Batianoff & Dillewaard 1996; Christodoulakis 1996; Lowry II 1996; Cronk 1997; Davis *et al.* 1997; Florence & Lorence 1997; Gabrielsen *et al.* 1997; Médail & Quézel 1997; Medail & Verlaque 1997; Baldini 1998; Chown *et al.* 1998; Médail & Vidal 1998; Stuessy *et al.* 1998; Sun & Stuessy 1998; Zanoni & Buck 1999; Baldini 2000; Barkalov 2000; Hobohm 2000; Moody 2000; Baldini 2001; Frodin 2001; Panitsa & Tzanoudakis 2001; Lawesson & Skov 2002; Pietsch *et al.* 2003; Dahl 2004; Meyer 2004; Price 2004; Roos *et al.* 2004; McMaster 2005; Trusty *et al.* 2006.

Text V.2.2. Data on isolation metrics of 453 islands worldwide may be downloaded from www.ecography.org/sites/ecography.org/files/appendix/e7669_weigelt_kreft_isolation.csv. The data comprise variations of seventeen metrics that performed best in spatial multi-predictor regression analyses including area, temperature, precipitation, elevational range and geology as co-predictors of vascular plant species richness (Table II.2.2) as well as eleven additional metric variations that might be of interest (D1b$_m$, D2g$_l$, stD6a$_m$, ^{stM}C7a$_m$, ^{stM}C10a$_l$, N16a, A17a$_l$, A17b$_l$, A17c$_l$, A17d$_l$, A17e$_l$). Raw data (not log-transformed) are provided as comma separated text file. The first line contains column headers. Metric nomenclature follows Fig. II.2.1 and Table II.2.1. Metrics indicated by the letter D are true distances measured in kilometres or weighted derivatives, other letters describe dimensionless metrics. Island names (Name), ISO 3166-1 country codes (ISO), corresponding English country names (Country), as well as latitude (LAT) and longitude (LON) of the mass centroids in decimal degrees are given.

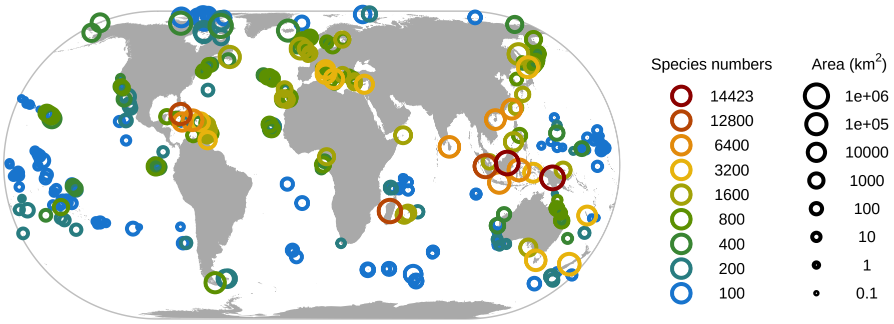

Figure V.2.1. Map of the 453 islands considered in Chapter II.2. Legend numbers for species richness refer to upper limits of classes. Symbol size is a linear function of log$_{10}$ island area.

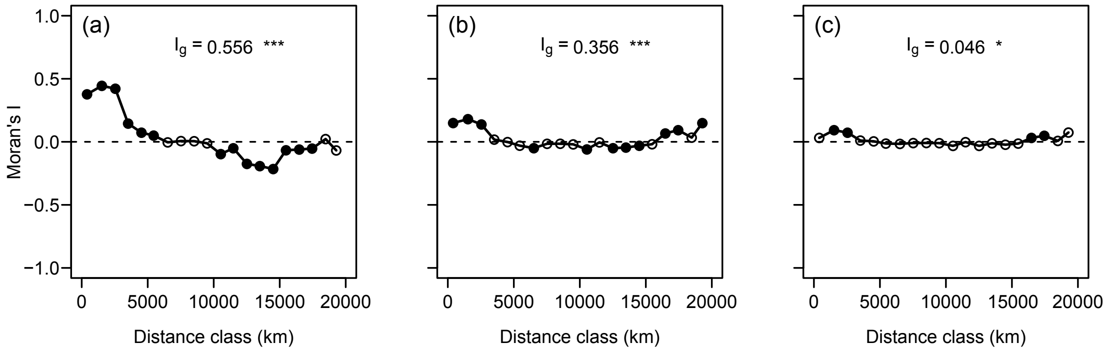

Figure V.2.2. Moran's I correlograms for vascular plant species richness on 453 globally distributed islands. Graphs show spatial autocorrelation of (a) log$_{10}$-transformed species richness, (b) residuals from non-spatial multi-predictor models (GLM) and (c) residuals from spatial multi-predictor models (SAR) both including area, temperature, precipitation, elevational range, geology and isolation measured as the proportion of surrounding landmass (A17l$_l$), as explanatory variables for plant species richness. Values of filled circles are significant at 5%-level. Significance of global Moran's I values (I_g): *** ($p < 0.001$), * ($p < 0.05$).

Table V.2.1. Calculation of seventeen isolation metrics in sixty-eight variations (indicated by minor letters) and their underlying hypotheses. Symbology follows Fig. II.2.1 and Table II.2.1. GIS analyses were performed in ArcGIS/ArcINFO Desktop 9.3.1 (ESRI, Redlands). Landmass polygons were extracted from the GADM database of global administrative areas (Hijmans *et al.* 2009).

Metric	Calculation	Hypothesis
$\mathbf{D1_m}$	shortest distance from a) target island mass centroid and b) coastline to mainland coastline (excluding Antarctica) using 'Generate Near Table' tool in ArcGIS; azimuthal equidistant map projection centred for target island.	continents are the most important source landmasses for immigration on islands.
$\mathbf{D2_l}$	shortest distance from target island coastline to coastline of a landmass of defined minimum area calculated like $\mathbf{D1b_m}$; varying minimum source area: a-f) 10^0-10^5 km^2; g-p) 1-10 times the target island area.	continents and islands, at least large ones, both serve as important sources for immigration on islands.
$\mathbf{U3} = D1b_m^{1/2} + D_a^{1/2} + D2g_l^{1/2}$	for 229 islands, isolation index obtained from UNEP Island Directory (http://islands.unep.ch/isldir.htm); missing values calculated according to Dahl (2004) as sum of square roots of distances to nearest equivalent or larger island ($\mathbf{D2g_l}$), nearest island group or archipelago (D_a) and nearest continent ($\mathbf{D1b_m}$); where one of these did not exist, next higher distance was repeated, except in the case of small satellite islands close to much larger landmasses; D_a measured according to UNEP Island Directory island group or archipelago affiliation.	continents and islands, at least large ones, both serve as important sources for immigration on islands; isolation can be explained as additively compound of distances to mainland, archipelagos and islands.
$\mathbf{D4_{cm}}$	shortest distance from target island coastline to climatically similar mainland area using 'Generate Near Table' tool in ArcGIS; azimuthal equidistant map projection centred for target island; source defined as areas being on average not more than 2°C colder than the minimum and not more than 2°C warmer than the maximum mean annual temperature on the target island and receiving not more than 20% less annual rainfall than the minimum and not more than 20% more than the maximum annual precipitation on the target island (WorldClim; Hijmans *et al.* 2005); for three high Arctic islands no climatically similar mainland area could be identified, distance to mainland was used instead.	only those parts of continents which are climatically similar to the target island serve as source areas for immigration to islands.
$\mathbf{D5_{cl}}$	shortest distance from target island coastline to climatically similar area on the landmass of defined minimum area calculated like $\mathbf{D4_{cm}}$; varying minimum source area: a-f) 10^0-10^5 km^2.	those parts of continents and at least large islands which are climatically similar to the target island serve as source areas.
$\mathbf{{}^{st}C6_m}$; $\mathbf{{}^{st}D6_m} = \sum {}^{ii}D_m$	shortest stepping stone distance from target island coastline to mainland coastline calculated using the 'Cost Distance' tool of the 'Spatial Analyst' in ArcGIS; analysis window radius = $\mathbf{D1b_m}$ + 1,000 km; the 'Cost Distance' tool calculated the least accumulative cost distance for each cell of a raster layer to the nearest source over a cost surface; the cost surface was a raster layer of 1 km^2 resolution considering all islands of at least 1 km^2 as stepping stones; using a higher resolution was not feasible due to computational limitations; costs were defined as a) 1 unit per km over water, 0 units per km over land ($\mathbf{{}^{st}D6a_m}$; sum of inter-island distances (${}^{ii}D_m$) in km) or b) 2 units per km over water, 1 unit per km over land ($\mathbf{{}^{st}C6b_m}$) double counting the distance over water.	stepping stones facilitate dispersal from source landmasses to the target island; continents are the most important source landmasses; a) only dispersal over water limits immigration on islands; b) dispersal over water limits immigration on islands more than dispersal over land.
$\mathbf{{}^{stM}C7_m}$; $\mathbf{{}^{stM}D7_m} = (\sum {}^{ii}D_m^x)/y$	stepping stone distance from target island coastline to mainland coastline on minimum inter-island distance path calculated by means of two consecutive 'Cost Distance' analyses (see above); first, calculation of cost distance raster using all landmass as source and a cost surface raster with costs of 1 unit per km over water and 0 units per km over land; second, calculation of cost distance raster for mainland as source using the first output cost distance raster + 1 as input cost surface, i.e. fixed costs of 1 unit per km over land and increasing costs with increasing distance to landmass coast over water; the second output cost distance raster shows exponentially increasing costs with increasing length of inter-island distances forcing the algorithm to find a stepping stone path of minimum inter-island distances (${}^{ii}D_m$); a least cost path was calculated using the 'Cost Path' tool; area (A) and number (#) of stepping stones were used in calculations of weighted stepping stone distances: a) costs derived from 'Cost Distance' analysis ($\mathbf{{}^{stM}C7_m}$); b-g) unweighted and weighted distances over water extracted from cost distance path ($\mathbf{{}^{stM}D7_m}$): b) x = 1, y = 1; c) x = 2, y = 1; d) x = 1, y = ∑ A; e) x = 2, y = ∑ A f) x = 1, y = # g) x = 2, y = #.	stepping stones facilitate dispersal from source landmasses to target island; continents are most important source landmasses; the length of the inter-island distances limits dispersal; b-g) x = 2: greater influence of larger distances; y = ∑ A: greater influence of large stepping stones; y = #: number of stepping stones important.

(continued on next page)

Metric	**Calculation**	**Hypothesis**
$\mathrm{max}^{ii}\mathbf{D8}_{\mathbf{m}}$	maximum inter island distance to mainland extracted from minimum inter-island distance path ($^{\mathbf{stM}}\mathbf{D7b}_{\mathbf{m}}$).	the length of the maximum inter-island distance between target island and mainland is critical in limiting immigration.
$^{\mathbf{st}}\mathbf{D9}_{\mathbf{l}} = \sum {}^{ii}D_l$	shortest stepping stone distance from target island coastline to coastline of landmass of at least 100,000 km² calculated like $^{\mathbf{st}}\mathbf{D6a}_{\mathbf{m}}$; $^{ii}D_l$ = inter-island distances.	stepping stones facilitate dispersal from source landmasses to target island; continents and very large islands serve as sources.
$^{\mathbf{stM}}\mathbf{C10}_{\mathbf{l}}$; $^{\mathbf{stM}}\mathbf{D10}_{\mathbf{l}} = (\sum {}^{ii}D_l{}^x)/y$	stepping stone distance from target island coastline to coastline of landmass of at least 100,000 km² on minimum inter-island distance path calculated like $^{\mathbf{stM}}\mathbf{C7}_{\mathbf{m}}$ and $^{\mathbf{stM}}\mathbf{D7}_{\mathbf{m}}$; $^{ii}D_l$ = inter-island distances; a) costs derived from cost distance analysis ($^{\mathbf{stM}}\mathbf{C10}_{\mathbf{l}}$); b-g) unweighted distances over water and distances weighted by area (A) or number of stepping stones (#) extracted from cost distance path ($^{\mathbf{stM}}\mathbf{C10}_{\mathbf{l}}$): b) x = 1, y = 1; c) x = 2, y = 1; d) x = 1, y = ∑ A; e) x = 2, y = ∑ A f) x = 1, y = # g) x = 2, y = #.	stepping stones facilitate dispersal from source landmasses to the target island; continents and very large islands serve as sources; the length of the inter-island distances limits dispersal; b-g) a = 2: greater influence of larger distances; y = ∑ A: greater influence of large stepping stones; y = #: number of stepping stones important.
$\mathrm{max}^{ii}\mathbf{D11}_{\mathbf{l}}$	maximum inter island distance to landmass of at least 100,000 km² extracted from minimum inter-island distance path ($^{\mathbf{stM}}\mathbf{D10b}_{\mathbf{l}}$).	the length of the maximum inter-island distance between target island and large landmasses is critical in limiting immigration.
$^{\mathbf{W}}\mathbf{C12}_{\mathbf{m}}$	distance to mainland corrected for prevailing winds calculated using the 'Path Distance' tool of the 'Spatial Analyst' in ArcGIS; 'Path Distance' allows to incorporate a horizontal factor in the calculation of cost distances (see above) accounting for horizontal friction; the horizontal factor was calculated from a raster layer of horizontal wind directions using a linear function of the angle between the wind direction and the target (in ArcGIS: horizontal relative moving angle (HRMA); zero factor = 0.5, cut angle = 181, slope = 0.011); costs of the cost surface raster were set to 1 unit per km; analysis window radius = $\mathbf{D1b}_{\mathbf{m}}$ + 1,000 km; prevailing wind directions at water and land surface averaged over 10 years were calculated from monthly means of zonal and meridional wind speed vectors taken from the NCEP/NCAR Reanalysis Project (Kistler *et al.* 2001) for the time period from 1981 to 1990 at 2.5° resolution. Data were downscaled to 1 km² resolution.	prevailing winds affect dispersal probabilities between mainland and target island.
$^{\mathbf{C}}\mathbf{C13}_{\mathbf{m}}$	distance to mainland corrected for prevailing ocean currents calculated like $^{\mathbf{W}}\mathbf{C12}_{\mathbf{m}}$; prevailing ocean current directions at water surface averaged over 10 years were calculated from three-day means of zonal and meridional velocity vectors at 0.25° resolution for the period from 1997 to 2006 taken from the NASA project ECCO2 (Menemenlis *et al.* 2008) Data were downscaled to 1 km² resolution.	prevailing ocean currents affect dispersal probabilities between mainland and target island.
$^{\mathbf{stW}}\mathbf{C14}_{\mathbf{m}}$	stepping stone distance to mainland corrected for prevailing winds calculated like $^{\mathbf{W}}\mathbf{C12}_{\mathbf{m}}$; costs defined as 1 unit per km over water and 0 units per km over land.	prevailing winds affect dispersal probabilities between mainland and target island; stepping stones facilitate dispersal.
$^{\mathbf{stC}}\mathbf{C15}_{\mathbf{m}}$	stepping stone distance to mainland corrected for prevailing ocean currents calculated like $^{\mathbf{C}}\mathbf{C13}_{\mathbf{m}}$; costs defined as 1 unit per km over water and 0 units per km over land.	prevailing ocean currents affect dispersal probabilities between mainland and target island; stepping stones facilitate dispersal.
$\mathbf{N16} = \sum (A_l/(D_l + 1)^2)$	Neighbour Index of Kalmar and Currie (2006) calculated as the sum of the area of all neighbouring islands closer than the nearest mainland weighted by their squared distances; shortest distances from target island coastline to source island coastlines calculated like $\mathbf{D1b}_{\mathbf{m}}$; a) only islands closer than mainland; b) all islands; c) all landmass; d) all landmass ($\log_{10} A_l$).	all surrounding landmasses serve as sources for immigration on islands; contribution of potential source landmasses increases with area.
$\mathbf{A17}_{\mathbf{l}} = \sum (A_l/A_r)$	proportion of landmass in the surrounding of the target islands within defined buffer distance (from polygon perimeter); 'Buffer' tool in ArcGIS was applied at an azimuthal equidistant map projection centred for each target island; areas of clipped landmasses were calculated using a cylindrical equal area projection; buffer distances were selected covering the full range of possible distances at logarithmic scale starting at 1 km; a-e) varying buffer radius (r) from 10^0 to 10^4 km (n=1); f-o) sums of landmass proportions in all possible combinations of n=2 to n=5 consecutive buffer distances: f) 10^0-10^1 km; g) 10^1-10^2 km; h) 10^2-10^3 km; i) 10^3-10^4 km; j) 10^0-10^2 km; k) 10^1-10^3 km; l) 10^2-10^4 km; m) 10^0-10^3 km; n) 10^1-10^4 km; o) 10^0-10^4 km.	all surrounding landmasses serve as sources for immigration on islands; not only the distance to but the amount of available source land area nearby drives immigration rates; source coastline shape is important.

Table V.2.2. Matrix of Pearson's correlation coefficients among seventeen isolation metrics. Metric variations that showed highest model fits (AIC) in spatial multi-predictor models of vascular plant species richness on 453 globally distributed islands are presented here. See Fig. II.2.1 and Table II.2.1 for explanation of metric abbreviations. All correlations are significant with $p < 0.001$.

	log A17l$_{l}$	loglog N16$_{c}$	^{stC}C15$_{m}$	^{stW}C14$_{m}$	^{C}C13$_{m}$	^{W}C12$_{m}$	max^{ii}D11$_{l}$	^{stM}D10b$_{l}$	stD9$_{l}$	max^{ii}D8$_{m}$	^{stM}D7b$_{m}$	stC6b$_{m}$	D5e$_{cl}$	D4$_{cm}$	U3	D2f$_{l}$
D1a$_{m}$	-0.75	-0.87	0.98	0.94	0.98	0.91	0.63	0.96	0.96	0.69	0.97	1.00	0.87	0.93	0.88	0.96
D2f$_{l}$	-0.73	-0.84	0.96	0.92	0.95	0.87	0.70	0.97	0.99	0.78	0.95	0.96	0.89	0.90	0.87	
U3	-0.88	-0.94	0.86	0.84	0.87	0.84	0.74	0.82	0.86	0.74	0.85	0.87	0.78	0.85		
D4c$_{m}$	-0.74	-0.82	0.91	0.90	0.93	0.89	0.64	0.88	0.89	0.64	0.90	0.92	0.83			
D5ec$_{l}$	-0.67	-0.77	0.87	0.84	0.85	0.78	0.58	0.87	0.90	0.66	0.85	0.88				
stC6b$_{m}$	-0.75	-0.86	0.99	0.94	0.98	0.90	0.64	0.97	0.97	0.71	0.98					
^{stM}D7b$_{m}$	-0.73	-0.83	0.98	0.92	0.95	0.86	0.67	0.97	0.95	0.69						
max^{ii}D8$_{m}$	-0.61	-0.65	0.72	0.63	0.66	0.55	0.82	0.74	0.79							
stD9l	-0.72	-0.82	0.97	0.91	0.94	0.84	0.72	0.98								
^{stM}D10b$_{l}$	-0.68	-0.80	0.96	0.90	0.93	0.83	0.65									
max^{ii}D11$_{l}$	-0.61	-0.64	0.66	0.62	0.61	0.55										
^{W}C12$_{m}$	-0.73	-0.85	0.89	0.97	0.94											
^{C}C13$_{m}$	-0.73	-0.85	0.98	0.95												
^{stW}C14$_{m}$	-0.74	-0.84	0.94													
^{stC}C15$_{m}$	-0.73	-0.84														
loglog N16c	0.89															

Table V.2.3. Model fits of spatial simultaneous autoregressive models (SAR) for $\log_{10}$-transformed vascular plant species richness on 453 islands as response variable and different isolation metrics as explanatory variables. Models include one isolation metric variation, either alone (r^2) or in a multi-predictor framework (R^2) accounting for island area, temperature, precipitation, elevational range and geology. r^2_{sp} and R^2_{sp} accounting for spatial autocorrelation are shown in parentheses. For multi-predictor models, ΔAIC was calculated as the difference from the best model (AIC = 121.8). P-values in the multi-predictor models refer to estimates of the respective isolation metric. R^2_{pmvd} represents the absolute contribution of the respective isolation metric to the full model fit (R^2). See Fig. II.2.1 and Table II.2.1 for explanation of metric abbreviations. Significance: *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$), n.s. (not significant at $p \geq 0.05$).

	single-predictor models		multi-predictor models			
Isolation	**r^2 (r^2_{sp})**	**p**	**R^2 (R^2_{sp})**	**ΔAIC**	**P**	**R^2_{pmvd}**
D1a$_{m}$	0.240 (0.489)	***	0.786 (0.851)	29.3	***	0.152
D1b$_{m}$	0.254 (0.499)	***	0.785 (0.851)	30.6	***	0.155
D2a$_{l}$	0.084 (0.502)	***	0.728 (0.837)	79.4	***	0.016
D2b$_{l}$	0.159 (0.486)	***	0.728 (0.834)	84.4	***	0.018
D2c$_{l}$	0.200 (0.479)	***	0.743 (0.838)	71.3	***	0.045
D2d$_{l}$	0.201 (0.481)	***	0.756 (0.846)	46.3	***	0.080
D2e$_{l}$	0.227 (0.488)	***	0.770 (0.847)	43.0	***	0.110
D2f$_{l}$	0.264 (0.499)	***	0.786 (0.852)	26.7	***	0.158
log **D2g**$_{l}$	0.016 (0.517)	n.s.	0.736 (0.838)	74.9	***	0.022
log **D2h**$_{l}$	0.018 (0.517)	n.s.	0.736 (0.837)	75.9	***	0.023
log **D2i**$_{l}$	0.013 (0.520)	n.s.	0.732 (0.837)	76.1	***	0.021
log **D2j**$_{l}$	0.013 (0.520)	n.s.	0.733 (0.838)	75.0	***	0.022
log **D2k**$_{l}$	0.013 (0.520)	n.s.	0.734 (0.838)	75.3	***	0.022
log **D2l**$_{l}$	0.012 (0.522)	n.s.	0.732 (0.837)	77.8	***	0.020
log **D2m**$_{l}$	0.013 (0.522)	n.s.	0.734 (0.837)	76.7	***	0.021
log **D2n**$_{l}$	0.013 (0.523)	n.s.	0.734 (0.837)	77.4	***	0.021
log **D2o**$_{l}$	0.011 (0.525)	n.s.	0.734 (0.837)	78.0	***	0.020
log **D2p**$_{l}$	0.010 (0.529)	*	0.734 (0.837)	77.8	***	0.020
U3	0.231 (0.493)	***	0.795 (0.856)	15.9	***	0.151
D4$_{cm}$	0.262 (0.498)	***	0.776 (0.845)	49.8	***	0.111
log **D5a**$_{cl}$	0.253 (0.533)	***	0.726 (0.834)	87.0	***	0.019
log **D5b**$_{cl}$	0.264 (0.519)	***	0.733 (0.835)	83.3	***	0.033
D5c$_{cl}$	0.230 (0.485)	***	0.756 (0.842)	59.5	***	0.071
D5d$_{cl}$	0.258 (0.493)	***	0.774 (0.851)	31.9	***	0.115
D5e$_{cl}$	0.299 (0.513)	***	0.800 (0.856)	14.7	***	0.176
D5f$_{cl}$	0.287 (0.514)	***	0.792 (0.854)	20.5	***	0.175
st**D6a**$_{m}$	0.248 (0.495)	***	0.787 (0.851)	29.1	***	0.152
st**C6b**$_{m}$	0.253 (0.498)	***	0.786 (0.852)	27.0	***	0.158
log ^{stM}**C7a**$_{m}$	0.166 (0.489)	***	0.760 (0.842)	61.0	***	0.066
^{stM}**D7b**$_{m}$	0.249 (0.492)	***	0.783 (0.849)	35.9	***	0.133
log ^{stM}**D7c**$_{m}$	0.170 (0.489)	***	0.770 (0.846)	49.5	***	0.086
^{stM}**D7d**$_{m}$	0.006 (0.506)	n.s.	0.718 (0.832)	92.3	**	0.004
log ^{stM}**D7e**$_{m}$	0.042 (0.499)	n.s.	0.739 (0.833)	86.7	***	0.020
log ^{stM}**D7f**$_{m}$	0.120 (0.485)	***	0.758 (0.840)	65.8	***	0.054
log ^{stM}**D7g**$_{m}$	0.145 (0.485)	***	0.766 (0.843)	57.9	***	0.069
max^{ii}**D8**$_{m}$	0.138 (0.475)	***	0.778 (0.845)	49.8	***	0.074
st**D9**$_{l}$	0.264 (0.497)	***	0.793 (0.852)	24.4	***	0.161
^{stM}**C10a**$_{l}$	0.151 (0.478)	***	0.777 (0.847)	42.6	***	0.096
^{stM}**D10b**$_{l}$	0.230 (0.485)	***	0.778 (0.848)	37.8	***	0.122
log ^{stM}**D10c**$_{l}$	0.187 (0.494)	***	0.767 (0.844)	55.8	***	0.084
^{stM}**D10d**$_{l}$	0.006 (0.506)	n.s.	0.717 (0.832)	92.4	*	0.004
log ^{stM}**D10e**$_{l}$	0.030 (0.501)	n.s.	0.730 (0.832)	91.3	**	0.014
log ^{stM}**D10f**$_{l}$	0.124 (0.490)	***	0.746 (0.838)	73.6	***	0.046
log ^{stM}**D10g**$_{l}$	0.151 (0.490)	***	0.755 (0.840)	67.2	***	0.061

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	single-predictor models		multi-predictor models			
Isolation metric	**r^2 (r^2_{sp})**	**p**	**R^2 (R^2_{sp})**	**ΔAIC**	**P**	**R^2_{pmvd}**
max^{ii}**D11**$_l$	0.180 (0.483)	***	0.777 (0.845)	48.4	***	0.096
^{W}**C12**$_m$	0.254 (0.503)	***	0.763 (0.846)	44.8	***	0.123
^{C}**C13**$_m$	0.251 (0.501)	***	0.782 (0.851)	28.6	***	0.152
^{stW}**C14**$_m$	0.273 (0.502)	***	0.775 (0.849)	34.8	***	0.146
^{stC}**C15**$_m$	0.253 (0.499)	***	0.787 (0.853)	22.3	***	0.163
log **N16a**	0.147 (0.513)	***	0.718 (0.831)	93.7	*	0.006
log **N16b**	0.175 (0.513)	***	0.722 (0.833)	88.5	**	0.013
loglog **N16c**	0.253 (0.514)	***	0.786 (0.852)	28.9	***	0.151
N16d	0.079 (0.522)	***	0.714 (0.830)	97.8	n.s.	0.001
log **A17a**$_l$	0.009 (0.506)	n.s.	0.716 (0.832)	92.0	**	0.004
log **A17b**$_l$	0.002 (0.511)	n.s.	0.715 (0.831)	95.8	n.s.	0.002
log **A17c**$_l$	0.036 (0.498)	n.s.	0.732 (0.841)	67.7	***	0.026
log **A17d**$_l$	0.186 (0.486)	***	0.774 (0.850)	33.6	***	0.096
A17e$_l$	0.151 (0.472)	***	0.780 (0.845)	49.7	***	0.076
log **A17f**$_l$	0.004 (0.509)	n.s.	0.716 (0.831)	93.8	*	0.003
log **A17g**$_l$	0.028 (0.502)	n.s.	0.729 (0.839)	73.2	***	0.023
log **A17h**$_l$	0.146 (0.480)	***	0.777 (0.855)	21.5	***	0.101
log **A17i**$_l$	0.231 (0.489)	***	0.809 (0.858)	7.2	***	0.140
log **A17j**$_l$	0.031 (0.501)	n.s.	0.730 (0.839)	71.6	***	0.025
log **A17k**$_l$	0.128 (0.478)	***	0.772 (0.852)	29.2	***	0.096
log **A17l**$_l$	0.185 (0.479)	***	0.807 (0.861)	0.0	***	0.134
log **A17m**$_l$	0.130 (0.478)	***	0.773 (0.853)	27.1	***	0.100
log **A17n**$_l$	0.164 (0.475)	***	0.801 (0.858)	9.7	***	0.126
log **A17o**$_l$	0.165 (0.475)	***	0.802 (0.858)	8.1	***	0.128

Table V.2.4. Model fits of non-spatial models (GLM) with the $\log_{10}$-transformed number of vascular plant species on 453 islands as response variable and different isolation metrics as explanatory variables. The first model includes no isolation metrics, but only island area, temperature, precipitation, elevational range and geology, and is included for comparison. All other models include one isolation metric, either as a single predictor (r^2) or in a multi-predictor model including also island area, temperature, precipitation, elevational range and geology (R^2). Except for A17i$_l$ and N16c all single predictor relationships are negative. For multi-predictor models, ΔAIC was calculated as the difference from the best model (AIC = 229.6). P-values in the multi-predictor models refer to estimates of the respective isolation metric. See Fig. II.2.1 and Table II.2.1 for abbreviations. Significance: *** ($p < 0.001$).

	single-predictor models		multi-predictor models			
Isolation metric	**r^2**	**P**	**R^2**	**ΔAIC**	**P**	**R^2_{pmvd}**
-	-	-	0.718	182.0	-	-
D1a$_m$	0.240	***	0.787	57.2	***	0.141
D2f$_l$	0.264	***	0.787	56.4	***	0.145
U3	0.231	***	0.796	36.8	***	0.167
D4$_{cm}$	0.262	***	0.779	74.0	***	0.135
D5e$_{cl}$	0.299	***	0.801	25.6	***	0.182
st**D6a**$_m$	0.248	***	0.788	53.8	***	0.137
^{stM}**D7b**$_m$	0.249	***	0.784	62.2	***	0.133
max^{ii}**D8**$_m$	0.138	***	0.781	68.5	***	0.078
st**D9**$_l$	0.264	***	0.794	41.2	***	0.150
^{stM}**C10a**$_l$	0.151	***	0.782	66.6	***	0.083
max^{ii}**D11**$_l$	0.180	***	0.781	68.6	***	0.094
^{W}**C12**$_m$	0.254	***	0.764	102.5	***	0.114
^{C}**C13**$_m$	0.251	***	0.784	63.3	***	0.138
^{stW}**C14**$_m$	0.273	***	0.776	79.5	***	0.136
^{stC}**C15**$_m$	0.253	***	0.789	52.8	***	0.142
loglog **N16c**	0.253	***	0.789	52.9	***	0.180
log **N17i**$_l$	0.231	***	0.812	0.0	***	0.146

Table V.2.5. Best multi-predictor models (SAR) including (a) one, (b) two, or (c) three isolation metrics as explanatory variables in addition to area, temperature, precipitation, elevational range and geology. The response variable is $\log_{10}$-transformed vascular plant species richness on 453 globally distributed islands. R^2 of individual variables shows their absolute contribution to the full model R^2 calculated as R^2_{pmvd}. See Fig. II.2.1 and Table II.2.1 for metric abbreviations. Significance: *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$).

		Estimate	**SE**	**z**	**P**	**R^2 (R^2_{sp})**	**AIC**
(a)	**Full model**					0.807 (0.861)	121.8
	(Intercept)	-5.36	0.61	-8.81	***		
	Log area	0.30	0.02	19.20	***	0.439	
	Log elevation	0.09	0.03	3.06	**	0.023	
	Log temperature	2.81	0.33	8.52	***	0.067	
	Log precipitation	0.45	0.06	8.11	***	0.051	
	Geology					0.092	
	atoll	-	-	-	-		
	continental	0.42	0.08	5.57	***		
	volcanic	0.33	0.07	4.93	***		
	Isolation						
	log $\mathbf{A17I}_{I}$	2.06	0.20	10.52	***	0.134	
(b)	**Full model**					0.839 (0.871)	84.9
	(Intercept)	-5.25	0.58	-9.01	***		
	Log area	0.29	0.01	19.58	***	0.419	
	Log elevation	0.08	0.03	3.04	**	0.025	
	Log temperature	2.90	0.32	9.16	***	0.065	
	Log precipitation	0.43	0.05	8.11	***	0.047	
	Geology					0.066	
	atoll	-	-	-	-		
	continental	0.34	0.07	4.56	***		
	volcanic	0.26	0.06	4.14	***		
	Isolation						
	$\mathbf{D5e}_{cl}$	$-1.07e^{-04}$	$1.69e^{-05}$	-6.37	***	0.124	
	log $\mathbf{A17I}_{I}$	1.54	0.20	7.54	***	0.095	
(c)	**Full model**					0.847 (0.872)	81.5
	(Intercept)	-5.29	0.56	-9.49	***		
	Log area	0.29	0.01	19.52	***	0.418	
	Log elevation	0.08	0.03	3.12	**	0.025	
	Log temperature	2.94	0.30	9.72	***	0.065	
	Log precipitation	0.43	0.05	8.20	***	0.047	
	Geology					0.063	
	atoll	-	-	-	-		
	continental	0.33	0.07	4.53	***		
	volcanic	0.28	0.06	4.46	***		
	Isolation						
	$\max^{ii}\mathbf{D11}_{I}$	$-1.01e^{-04}$	$4.15e^{-05}$	-2.43	*	0.015	
	$\mathbf{D5e}_{cl}$	$-9.59e^{-05}$	$1.71e^{-05}$	-5.60	***	0.122	
	log $\mathbf{A17I}_{I}$	1.42	0.21	6.79	***	0.093	

Table V.2.6. Best non-spatial multi-predictor models (GLM) including (a) one, (b) two, or (c) three isolation metrics as explanatory variables in addition to area, temperature, precipitation, elevational range and geology. The response variable is $\log_{10}$-transformed vascular plant species richness on 453 globally distributed islands. R^2 of individual variables shows their absolute contribution to the full model R^2 calculated as R^2_{pmvd}. See Fig. II.2.1 and Table II.2.1 for explanation of metric abbreviations. Significance: *** ($p < 0.001$), ** ($p < 0.01$) , n.s. (not significant at $p \geq 0.05$).

		Estimate	SE	z	P	R^2	AIC
(a)	**Full model**					0.812	229.6
	(Intercept)	-6.19	0.40	-15.41	***		
	Log area	0.29	0.02	17.40	***	0.418	
	Log elevation	0.06	0.03	1.84	n.s.	0.009	
	Log temperature	3.19	0.22	14.66	***	0.072	
	Log precipitation	0.52	0.04	11.57	***	0.055	
	Geology					0.113	
	atoll	-	-	-	-		
	continental	0.56	0.06	9.04	***		
	volcanic	0.48	0.06	8.25	***		
	Isolation						
	log **A17i**$_{l}$	2.92	0.20	14.93	***	0.146	
(b)	**Full model**					0.846	143.0
	(Intercept)	-5.74	0.37	-15.63	***		
	Log area	0.28	0.02	18.35	***	0.406	
	Log elevation	0.07	0.03	2.59	**	0.018	
	Log temperature	3.08	0.20	15.58	***	0.067	
	Log precipitation	0.51	0.04	12.67	***	0.053	
	Geology					0.072	
	atoll	-	-	-	-		
	continental	0.37	0.06	6.18	***		
	volcanic	0.33	0.06	6.06	***		
	Isolation						
	D5e$_{cl}$	-1.17e^{-04}	1.19e^{-05}	-9.79	***	0.128	
	log **A17i**$_{l}$	2.18	0.19	11.28	***	0.102	
(c)	**Full model**					0.854	120.4
	(Intercept)	-5.74	0.36	-16.03	***		
	Log area	0.28	0.02	18.57	***	0.405	
	Log elevation	0.07	0.03	2.77	**	0.018	
	Log temperature	3.07	0.19	15.91	***	0.067	
	Log precipitation	0.51	0.04	12.93	***	0.053	
	Geology					0.080	
	atoll	-	-	-	-		
	continental	0.41	0.06	7.03	***		
	volcanic	0.39	0.06	7.11	***		
	Isolation						
	^{stM}**C10a**$_{l}$	-1.71e^{-10}	3.44e^{-11}	-4.97	***	0.020	
	D5e$_{cl}$	-8.87e^{-05}	1.29e^{-05}	-6.88	***	0.110	
	log **A17i**$_{l}$	2.02	0.19	10.59	***	0.100	

3. Supplementary information - Chapter II.3

Biogeographic, climatic and spatial drivers differentially affect alpha, beta and gamma diversity in oceanic archipelagos

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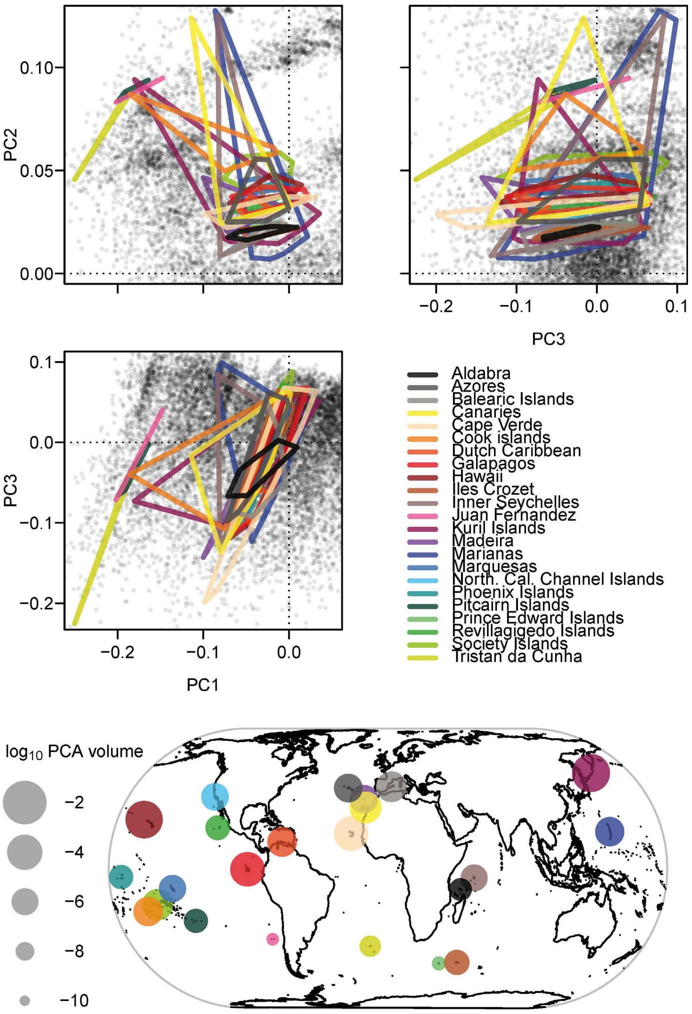

Figure V.3.1. Archipelagos and their environmental volume. We assessed 23 archipelagos, visualized as the minimum convex hull polygons comprising the islands of each archipelago in two dimensions of a global environmental island space (bi-plots). The global environmental island space (black dots) was derived from a principal component analysis (PCA) that included 17,883 islands worldwide and ten bioclimatic and physical variables (area, distance to the nearest mainland, surrounding landmass proportion, last glacial maximum mainland connection, elevational range, temperature, precipitation, seasonality in temperature and precipitation, and past climate change velocity in temperature); for details see Weigelt *et al.* (2013a). We calculated a measure of each archipelago's environmental heterogeneity among its constituent islands as the volume of a three dimensional convex hull (see Barber *et al.* 1996) comprising the islands of each archipelago along the first three axes of the PCA space (containing 72.4% cumulative variation; $\log_{10}$ PCA volume in map). This measurement is termed environmental volume in the main text. For archipelagos with less than four islands, we replaced each point in the PCA by a small cube of 0.0001 PCA units edge length.

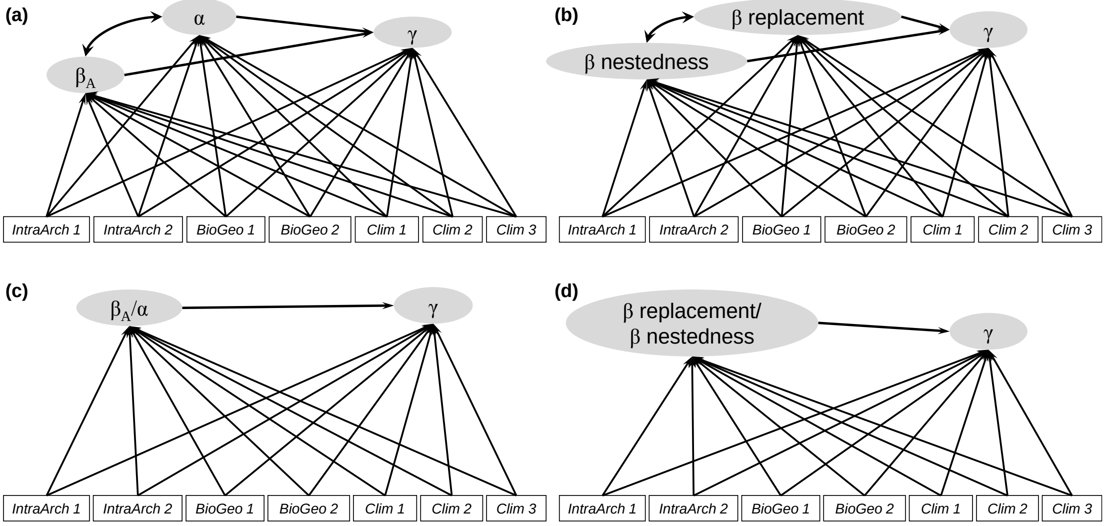

Figure V.3.2. Full structural equation models (SEMs) used as starting points to model direct and indirect effects of biogeographic, climatic, and intra-archipelagic factors on γ diversity of vascular plants on 23 oceanic archipelagos worldwide. Diversity components and ratios (in grey) were the response variables and main axes of principal components analyses of abiotic variables were the explanatory variables. The SEMs differed in the response variables and their relationships: (a) α and β_A components influencing γ diversity; (b) β replacement and β nestedness influencing γ diversity; (c) the β_A/α ratio influencing γ diversity; and (d) the β replacement/ β nestedness ratio influencing γ diversity. Explanatory variables refer to axes of the three principal component analyses performed separately for biogeographic (*BioGeo 1–2*), climatic (*Clim 1–3*), and intra-archipelagic (*IntraArch 1–2*) variables.

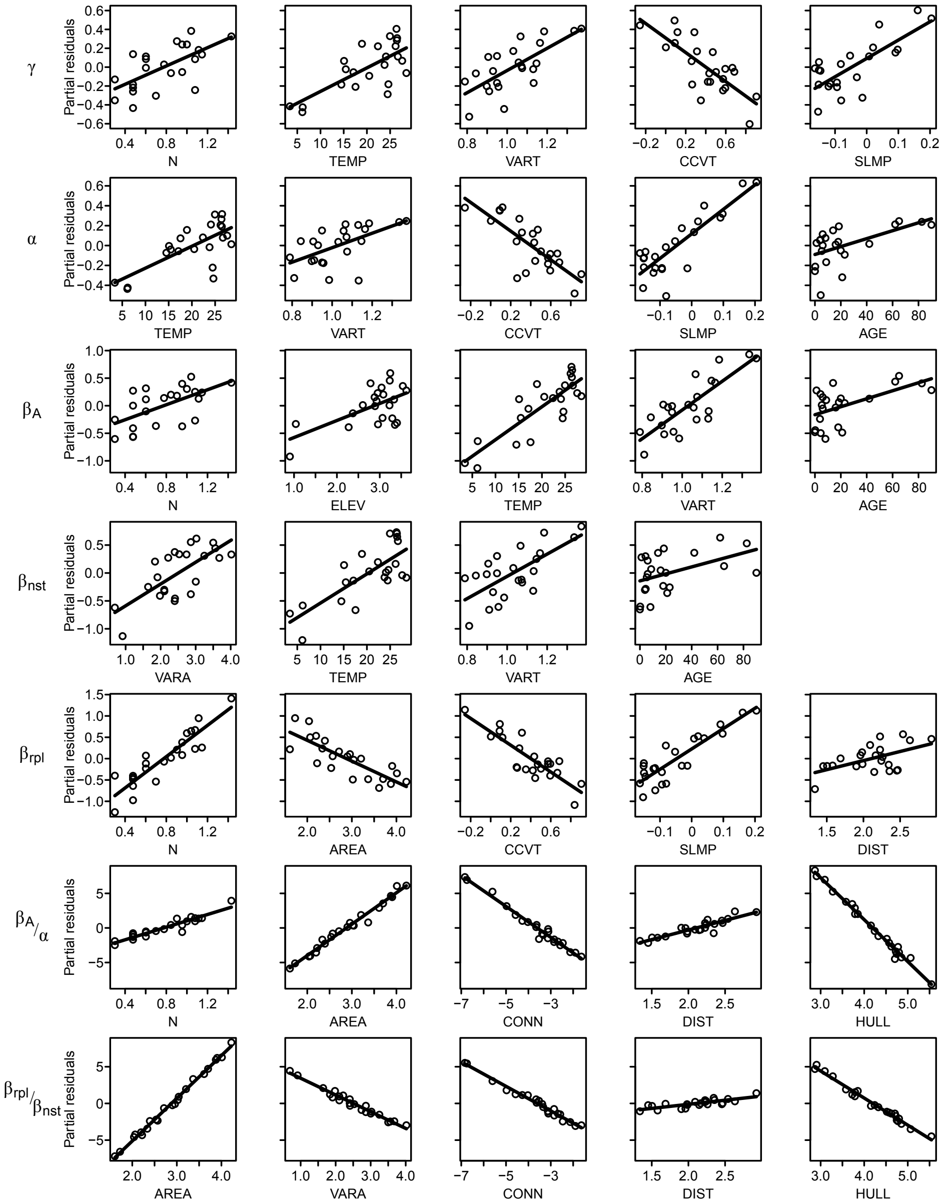

Figure V.3.3. Partial residual plots for minimum adequate models from ordinary least-square regressions for diversity components. Plant diversity components and their ratios were used as response variables and environmental variables as explanatory variables on 23 oceanic archipelagos worldwide. Model selection was based on values of the Akaike Information Criterion corrected for small sampling sizes (AIC_c) of models with all possible factor combinations. Explanatory variables were standardized (zero mean, unit variance), except age (given in million years) and temperature (in ˚C). *AREA* - total land area; *SLMP* - surrounding landmass proportion; *AGE* - age of the oldest island; *ELEV* - maximum island elevation; *TEMP* - annual mean temperature; *VART* - variation in annual temperature (range); *CCVT* - Late Quaternary climate change velocity of temperature; *VARA* - variation in island area (range); N - number of islands; *HULL* - archipelago hull; *CONN* - connectivity; *DIST* - mean inter-island distance.

Table V.3.1. Studied archipelagos (n = 23) and diversity data. We used the additive partitioning of γ diversity, with the α component being the mean richness of the island floras within each archipelago (see main text). Beta replacement (β_{rpl}) and β nestedness (β_{nst}) followed Chiarucci *et al.* (2010). Small islands that geologically belong to a neighbouring larger island or to an atoll (e.g. To'opua to Bora Bora, Society Islands; or Ford island in the harbour of Honolulu to Oahu, Hawaiian islands) and therefore did not have their own species lists were considered as part of the larger island or of the atoll, respectively. Three small islands with missing climate data had to be excluded (Marianne, Seychelles; Santa Clara, Juan Fernandez; and Rashuwa, Kuril Islands). Island-level data may be downloaded from dx.doi.org/10.5061/dryad.3jv54.

Archipelago	**Source**	α	β_A	β_{rpl}	β_{nst}	γ
Hawaii	Wagner *et al.* 2005; Athens *et al.* 2007	286.75	905.25	565	340.25	1192
Galapagos	Jaramillo Díaz & Guézou 2011	185.08	348.92	135	213.92	534
Cape Verde	Arechavaleta *et al.* 2005	100.42	143.58	67	76.58	244
Azores	Borges *et al.* 2005	181.40	80.60	49	31.60	262
Madeira	Borges *et al.* 2008	390.70	304.30	37	267.30	695
Canaries	Arechavaleta *et al.* 2009	677.71	701.29	412	289.29	1379
Marquesas	Wagner & Lorence 2002; Florence *et al.* 2007	166.00	228.00	100	128.00	394
Juan Fernandez	Marticorena *et al.* 1998	130.50	69.50	54	15.50	200
Prince Edward Islands	Greene & Walton 1975; Shaw *et al.* 2010	25.50	1.50	0	1.50	27
Tristan da Cunha	Wace & Dickson 1965; Shaw *et al.* 2010	77.30	26.70	9	17.70	104
Iles Crozet	Greene & Walton 1975; Shaw *et al.* 2010	21.70	9.30	3	6.30	31
Pitcairn Islands	Kingston *et al.* 2003; Florence *et al.* 2007	54.25	91.75	37	54.75	146
Revillagigedo Islands	Johnston 1931; Levin & Moran 1989	67.30	98.70	17	81.70	166
Northern CA Channel Islands	Junak *et al.* 1997	310.25	232.75	74	158.75	543
Cook Islands	Florence *et al.* 2007; The Cook Islands Natural Heritage Trust 2007; University of Kent 2012	110.75	190.25	37	153.25	301
Dutch Caribbean	CARMABI 2009	441.70	145.30	38	107.30	587
Aldabra	Renvoize 1975; Fosberg *et al.* 1980; Gerlach 2003	177.25	122.75	24	98.75	300
Phoenix Islands	Stoddart & Fosberg 1994	20.60	7.40	4	3.40	28
Kuril Islands	Tatewaki 1957; Egorova 1964; Chernyaeva 1973; Takahashi *et al.* 1997; Takahashi *et al.* 1999; Takahashi *et al.* 2002; Gage *et al.* 2006; Takahashi *et al.* 2006; Burke Museum of Natural History and Culture 2012	186.40	1043.60	602	441.60	1230
Balearic Islands	Sáez & Rosselló 2001; UIB 2007	618.30	671.70	167	504.70	1290
Society Islands	Fosberg & Sachet 1987; Florence *et al.* 2007	164.80	486.20	173	313.20	651
Inner Seychelles	Hill 2002; Gerlach 2003	146.00	299.00	106	193.00	445
Marianas	Fosberg 1958; Raulerson 2006	138.30	368.70	88	280.70	507

Table V.3.2. Pearson's correlations among diversity components of vascular plants on 23 oceanic archipelagos worldwide. Diversity components were measured in species numbers (i.e. species richness). Significant correlations are shown in bold. Correlations were calculated for $\log_{10}$-transformed variables, except for the ratios. β_{rpl} = β_A replacement; β_{nst} = β_A nestedness. Significance: ** $0.01>P>0.001$; $^{***}P<0.001$

	α	β_A	β_{rpl}	β_{nst}	β_A/α	β_{rpl}/β_{nst}
β_A	**0.83*****					
β_{rpl}	**0.81*****	**0.98*****				
β_{nst}	**0.77*****	**0.96*****	**0.88*****			
β_A/α	0.20	**0.65*****	**0.61****	**0.68*****		
β_{rpl}/β_{nst}	0.09	0.10	−0.11	0.33	0.10	
γ	**0.93*****	**0.97*****	**0.95*****	**0.92*****	**0.54****	0.10

Table V.3.3. Studied archipelagos (n = 23) and biogeographic variables. References for sources of age estimates of the oldest island are also provided (see main text for references of remaining variables). Mean island area and mean elevation of the archipelagos were calculated from the planar land area of each island and from digital elevation models, respectively. Distance to mainland was calculated as the shortest distance of the islands' mass centroids to the nearest continent coast. Mean area, distance to mainland and mean elevation were not included in the final analyses to avoid collinearity (see Table V.3.6) and model overfitting. Island-level data may be downloaded from dx.doi.org/10.5061/dryad.3jv54.

Archipelago	Land area (km^2)	Mean island area (km^2)	log$_{10}$ surrounding landmass proportion	Distance to mainland (km)	Age of oldest island (my)	References for age estimates	Maximum elevation (m)	Mean elevation (m)
Hawaii	16732	1394	−0.121	3162	23.0	8, 10, 11, 19	4176	1087
Galapagos	8031	618	−0.152	948	3.9	1, 3, 17 - 19, 21, 31, 37	1685	580
Cape Verde	4089	341	−0.014	587	21.0	15, 16, 19, 23,	2517	736
Azores	2323	258	−0.031	1385	8.1	6	2260	978
Madeira	796	265	0.040	603	14.0	6, 38	1755	818
Canaries	7510	1073	0.098	117	20.0	6	3450	1677
Marquesas	1103	123	−0.146	4754	6.0	5, 13, 19, 27	1103	741
Juan Fernandez	110	55	−0.082	609	6.0	25	842	701
Prince Edward Islands	344	172	−0.094	1720	0.22	29	1161	864
Tristan da Cunha	116	39	−0.116	2777	18.0	7, 19	1962	862
Iles Crozet	371	124	−0.094	2384	8.7	20	892	819
Pitcairn Islands	53	13	−0.151	4969	16.0	24	236	71
Revillagigedo Islands	166	55	−0.081	404	4.5	4	908	424
Northern CA Channel Islands	515	129	0.161	24	1.2	32	609	340
Cook Islands	218	27	−0.163	4747	18.0	19, 22, 26, 39	402	95
Dutch Caribbean	905	302	0.091	35	90.0	2	188	150
Aldabra	158	39	0.020	629	65.0	19, 25, 34	11	7
Phoenix Islands	41	8	−0.153	4158	0.0075	28	8	5
Kuril Islands	10253	380	0.008	26	82.0	33	2153	770
Balearic Islands	5022	837	0.205	89	5.3	36	1212	377
Society Islands	1610	146	−0.151	5677	4.3	12, 14, 19, 30, 35	1709	427
Inner Seychelles	248	25	−0.052	1206	62.0	9	757	177
Marianas	1051	75	−0.115	2233	42.0	19	774	379

References for age estimates: 1. Bailey (1976), 2. Beardsley & Avé Lallemant (2007), 3. Bow & Geist (1992), 4. Brattstrom (1990), 5. Brousse *et al.* (1990), 6. Cardoso *et al.* (2010), 7. Chevallier *et al.* (1992), 8. Clague *et al.* (2010), 9. Collier *et al.* (2008), 10. Dalrymple *et al.* (1981), 11. Dalrymple *et al.* (1977), 12. Duncan *et al.* (1994), 13. Duncan *et al.* (1986), 14. Duncan & McDougall (1976), 15. Duprat *et al.* (2007), 16. Dyhr & Holm (2010), 17. Geist *et al.* (1985), 18. Geist *et al.* (1986), 19. Gillespie & Clague (2009), 20. Giret *et al.* (2003), 21. Hall (1983), 22. Hein *et al.* (2004), 23. Holm *et al.* (2008), 24. Kingston *et al.* (2003), 25. Kueffer *et al.* (2010), 26. Lambeck (1981), 27. Legendre *et al.* (2006), 28. Maragos *et al.* (2008), 29. Quilty (2007), 30. Sedov *et al.* (2008), 31. Simkin (1984), 32. Sorlien (1994), 33. Tomilov (2000), 34. Trudgill (1979), 35. Uto *et al.* (2007), 36. van der Made *et al.* (2006), 37. Vicenzi *et al.* (1990), 38. Whittaker & Fernández-Palacios (2007), 39. Wood (1967).

Table V.3.4. Studied archipelagos (n= 23) and climatic variables. See main text for sources. Late Quaternary (LQ) climate change velocity of precipitation was tallied similarly as for temperature (see main text), but was excluded in the analyses to avoid overfitting of the statistical models and because of greater uncertainty in past precipitation data compared to past temperature data. Island-level data may be downloaded from dx.doi.org/10.5061/dryad.3jv54.

Archipelago	Annual mean temperature (˚C)	Annual precipitation (mm year^{-1})	Annual temperature range (˚C)	Coefficient of variation of precipitation	LQ climate change velocity in temperature (m y^{-1})	LQ climate change velocity in precipitation (m y^{-1})
Hawaii	23.8	2590.4	11.9	39.0	0.553	2.954
Galapagos	24.1	1056.5	11.4	28.8	1.234	3.233
Cape Verde	24.5	282.9	9.6	141.5	2.246	1.200
Azores	17.5	1385.7	13.5	35.8	2.636	5.308
Madeira	18.9	658.3	11.7	64.0	1.934	6.139
Canaries	20.5	412.4	14.0	80.8	1.004	4.746
Marquesas	26.5	1686.1	7.0	24.8	1.312	37.445
Juan Fernandez	15.4	1044.5	14.6	57.5	2.052	10.280
Prince Edward Islands	6.1	2642.5	9.0	7.0	2.783	7.720
Tristan da Cunha	14.5	1999.3	11.8	12.3	2.722	9.052
Iles Crozet	6.2	2556.7	8.9	12.7	3.932	13.647
Pitcairn Islands	22.4	1482.0	10.7	10.2	4.848	100.975
Revillagigedo Islands	24.6	288.0	13.6	94.7	1.839	3.161
Northern CA Channel Islands	15.1	475.0	15.3	97.2	4.635	40.318
Cook Islands	25.0	1921.4	8.9	40.5	2.954	86.217
Dutch Caribbean	27.6	543.7	8.1	61.0	3.737	2.233
Aldabra	26.2	1060.5	8.5	72.5	8.054	49.975
Phoenix Islands	28.5	943.0	6.5	35.6	6.885	16.522
Kuril Islands	3.4	1509.2	23.5	27.4	3.741	14.820
Balearic Islands	17.1	621.2	21.6	46.2	3.177	3.220
Society Islands	26.4	2222.7	8.0	44.6	1.226	28.220
Inner Seychelles	26.4	2152.6	6.2	47.6	3.937	35.378
Marianas	26.7	1974.2	7.9	46.7	1.815	125.114

Table V.3.5. Studied archipelagos (n= 23) and intra-archipelagic spatial variables. See main text for sources. The climatic and geographical environmental volumes were quantified as the volumes occupied by the islands of each archipelago in the ordination space of principal component analyses (PCA, axes 1–3) which included 17,883 islands worldwide and five bioclimatic or five physical variables from Weigelt et al. (2013a), respectively (see Fig. V.3.1). Proportion of land area was tallied as the ratio between island area (Table V.3.3) and archipelago hull. Climatic and geographical environmental volumes as well as proportion of land area were excluded from the final analyses to due to collinearity (see Table V.3.6) and to prevent overfitting of the statistical models. Island-level data may be downloaded from dx.doi.org/10.5061/dryad.3jv54.

Archipelago	Island area range (km^2)	Environ-mental volume	Climatic environmental volume	Geographic environmental volume	No. of islands	Archipelago hull (km^2)	Prop. of land area (%)	Connec-tivity	Mean inter-island distance (km)
Hawaii	10456	3.82^{-4}	1.00^{-4}	2.18^{-5}	12	349401	4.8	2.2^{-4}	845
Galapagos	4726	8.12^{-5}	1.12^{-5}	2.10^{-4}	13	53134	15.1	2.6^{-3}	122
Cape Verde	1007	7.07^{-5}	1.08^{-5}	6.78^{-5}	12	55945	7.3	7.4^{-4}	139
Azores	728	2.97^{-6}	4.08^{-7}	4.19^{-6}	9	50655	4.6	3.0^{-4}	220
Madeira	727	2.87^{-6}	6.22^{-8}	8.22^{-6}	3	3815	20.9	1.4^{-3}	37
Canaries	1767	1.67^{-5}	6.83^{-7}	1.02^{-4}	7	62991	11.9	2.1^{-3}	174
Marquesas	338	1.40^{-5}	1.17^{-7}	4.90^{-7}	9	21151	5.2	4.6^{-4}	146
Juan Fernandez	4	3.34^{-10}	3.07^{-10}	4.01^{-10}	2	1903	5.8	4.1^{-4}	168
Prince Edward Islands	251	8.23^{-10}	1.79^{-10}	9.74^{-10}	2	741	46.4	1.3^{-2}	21
Tristan da Cunha	95	4.91^{-8}	5.64^{-9}	5.24^{-8}	3	808	14.4	1.4^{-3}	27
Iles Crozet	80	4.36^{-7}	1.22^{-8}	2.20^{-6}	3	5325	7.0	7.8^{-4}	79
Pitcairn Islands	43	2.37^{-7}	1.20^{-8}	9.99^{-7}	4	37310	0.1	1.5^{-7}	345
Revillagigedo Islands	127	2.89^{-7}	4.11^{-8}	2.87^{-7}	3	14278	1.2	1.1^{-5}	285
Northern CA Channel Islands	252	1.62^{-6}	4.63^{-8}	4.43^{-7}	4	1244	41.4	2.3^{-2}	31
Cook Islands	68	4.44^{-6}	1.08^{-6}	1.72^{-6}	8	59773	0.4	2.5^{-6}	181
Dutch Caribbean	256	5.11^{-6}	1.24^{-7}	5.20^{-5}	3	6110	14.8	3.4^{-3}	90
Aldabra	126	1.04^{-7}	6.21^{-9}	4.35^{-6}	4	6170	2.6	5.4^{-5}	95
Phoenix Islands	7	2.41^{-7}	1.13^{-7}	1.32^{-7}	5	42075	0.1	1.8^{-7}	226
Kuril Islands	3174	5.93^{-4}	6.70^{-6}	1.08^{-3}	27	116349	8.8	7.6^{-4}	430
Balearic Islands	3635	9.38^{-6}	5.67^{-7}	2.91^{-5}	6	17383	28.9	7.4^{-3}	96
Society Islands	1051	1.25^{-5}	2.61^{-6}	2.60^{-5}	11	33065	4.9	2.3^{-4}	168
Inner Seychelles	163	1.14^{-6}	2.50^{-8}	3.45^{-6}	10	7124	3.5	9.5^{-5}	48
Marianas	547	3.98^{-6}	3.80^{-7}	1.77^{-5}	14	71593	1.5	2.7^{-5}	292

Table V.3.6. Pearson's correlations among abiotic factors. Significant correlations are given in bold, with the respective P-values in the lower part of the table. Variables' calculations and sources can be found in the main text and in Tables V.3.3, V.3.4 & V.3.5. A_l = island area; A_m = mean island area; D_c = distance to nearest continent; O = surrounding landmass proportion; M = age of the oldest island; E_m = mean elevation; E_a = maximum elevation; T_0 = annual mean temperature; P_0 = annual mean precipitation; T_s = annual temperature range; P_s = coefficient of variation of precipitation; V_t = Late Quaternary climate change velocity of temperature; V_p = Late Quaternary climate change velocity of precipitation; N = number of islands; A_r = range of island area; D_i = mean inter-island distance; H_c = climatic environmental volume; H_g = geographic environmental volume; H_t = environmental volume; C = connectivity; A_h = archipelago hull; A_p = proportion of land area. Significance: * 0.05>P>0.01; ** 0.01>P>0.001; ***P<0.001.

	A_p	A_h	C	H_t	H_g	H_c	D_i	A_r	N	V_p	V_t	P_s	T_s	P_0	T_0	E_a	E_m	M	O	D_c	A_m	A_l
A_l	**0.52**	**0.54**	**0.54**	**0.78**	**0.72**	**0.77**	0.29	**0.93**	**0.66**	**−0.48**	**−0.62**	0.24	**0.42**	−0.06	−0.11	**0.65**	**0.59**	0.13	0.32	−0.35	**0.92**	1
A_m	**0.70**	0.28	**0.72**	**0.57**	**0.53**	**0.55**	0.10	**0.86**	0.32	**−0.65**	**−0.61**	0.21	**0.50**	−0.15	−0.24	**0.66**	**0.67**	0.03	**0.46**	**−0.45**	1	***
D_c	**−0.53**	0.15	**−0.55**	−0.24	−0.33	−0.08	0.15	−0.28	0.01	0.35	−0.18	**−0.46**	**−0.62**	**0.62**	0.30	−0.10	−0.15	**−0.42**	**−0.86**	1	*	
O	**0.57**	−0.23	**0.57**	0.18	0.29	0.01	−0.31	0.30	−0.13	−0.33	0.21	**0.49**	**0.53**	**−0.6**	−0.21	0.07	0.11	0.25	1	***	*	
M	0.02	0.12	0.02	0.28	**0.45**	0.12	0.11	0.13	0.27	0.08	0.29	0.17	−0.07	−0.01	0.08	−0.20	−0.20	1		*		
E_m	**0.64**	−0.01	**0.64**	0.20	0.10	0.18	−0.07	**0.51**	0.14	**−0.43**	**−0.69**	−0.08	**0.43**	0.13	**−0.46**	**0.96**	1				***	**
E_a	**0.55**	0.14	**0.54**	0.35	0.22	0.34	0.02	**0.61**	0.30	−0.40	**−0.73**	−0.04	**0.44**	0.16	−0.36	1	***				***	***
T_0	**−0.49**	0.37	**−0.47**	0.20	0.20	0.30	0.29	−0.05	0.20	0.12	−0.15	**0.47**	**−0.57**	−0.24	1		*					
P_0	−0.08	0.02	−0.09	−0.13	−0.20	−0.09	0.01	0.00	0.14	0.39	−0.15	**−0.7**	−0.36	1					**	**		
T_s	0.40	0.05	0.39	0.21	0.17	0.17	0.14	0.37	0.06	−0.35	−0.11	0.12	1		**	*	*		**	**	*	*
P_s	0.06	0.19	0.09	0.33	0.34	0.35	0.15	0.15	0.18	−0.25	−0.12	1		***	*				*	*		
V_t	−0.26	−0.39	−0.27	−0.36	−0.2	**−0.48**	−0.33	**−0.56**	−0.32	0.36	1					***	***				**	**
V_p	**−0.48**	−0.04	**−0.49**	−0.23	−0.18	−0.27	0.03	−0.40	0.08	1							*				***	*
N	−0.11	**0.80**	−0.07	**0.81**	**0.73**	**0.82**	**0.54**	**0.62**	1													***
A_r	**0.51**	**0.48**	**0.50**	**0.78**	**0.74**	**0.73**	0.19	1	**		**					**	*				***	***
D_i	**−0.60**	**0.86**	**−0.50**	**0.46**	0.37	**0.57**	1		**													
H_c	−0.03	**0.84**	0.00	**0.95**	**0.82**	1	**	***	***		*										**	***
H_g	0.09	**0.67**	0.11	**0.93**	1	***		***	***									*			**	***
H_t	0.07	**0.75**	0.10	1	***	***	*	***	***												**	***
C	**0.99**	**−0.40**	1				**	*		*					*	**	***		**	**	***	**
A_h	**−0.44**	1		***	***	***	***	*	***													**
A_p	1	*	***				**	*		*					*	**	***		**	**	***	*

Table V.3.7. Pearson's correlations among abiotic factors and diversity components. Diversity was measured in species numbers. Significant correlations are in bold. All variables were log-transformed, except for the diversity ratios (β_A/α and β_{rpl}/β_{nst}), mean temperature, mean precipitation, absolute latitude and age. Discarded variables are shown in italic font; β_{rpl} = β replacement; β_{nst} = β nestedness; Significance: **.** 0.1>*P*>0.05; * 0.05>*P*>0.01; ** 0.01>*P*>0.001; ****P*<0.001.

Variable (unit)	α	β_A	β_A/α	β_{rpl}	β_{nst}	β_{rpl}/β_{nst}	γ
Biogeographic							
Island area (m^2)	**0.62****	**0.65*****	**0.50***	**0.62****	**0.71*****	0.11	**0.7*****
Mean island area (m^2)	**0.63****	**0.49***	0.22	**0.46***	**0.53****	0.10	**0.6 ****
Distance to nearest continent (m)	**-0.57****	-0.36 **.**	-0.09	-0.35 **.**	-0.33	-0.04	**-0.47***
Surrounding landmass proportion	**0.66*****	0.33	-0.16	0.35	0.26	-0.09	**0.47***
Age of oldest island (million years)	0.29	0.32	0.38 **.**	0.34	0.28	-0.08	0.36 **.**
Mean elevation (m)	0.28	0.23	0.17	0.19	0.29	0.20	0.29
Maximum elevation m	0.33	0.38 **.**	0.32	0.34	**0.43***	0.16	0.40 **.**
Climatic							
Annual mean temperature (˚C)	0.20	0.29	-0.04	0.32	0.22	-0.12	0.22
Annual mean precipitation (mm y^{-1})	**-0.42***	-0.24	0.24	-0.24	-0.18	-0.06	-0.28
Annual range in temperature (˚C)	**0.42***	0.36 **.**	0.26	0.30	0.39 **.**	0.30	**0.42***
Coefficient of variation of precipitation	**0.56****	**0.53****	0.05	**0.51***	**0.46***	0.13	**0.52***
Climate change velocity of temperature (m y^{-1})	-0.36 **.**	**-0.44***	-0.29	-0.39 **.**	**-0.49***	-0.25	**-0.44***
Climate change velocity of precipitation (m y^{-1})	-0.24	-0.02	0.17	0.03	-0.06	-0.17	-0.11
Intra−archipelagic							
Number of islands	0.29	**0.65*****	**0.79*****	**0.62****	**0.72*****	0.07	**0.55****
Range in island area (m^2)	**0.60****	**0.65*****	**0.50***	**0.67*****	**0.64****	-0.18	**0.69*****
Mean inter−island distance (m)	0.06	**0.42***	**0.59****	0.31	**0.51***	**0.43***	0.29
Climatic environmental volume	**0.42***	**0.68*****	**0.62****	**0.66*****	**0.71*****	0.02	**0.61****
Geographic environmental volume	**0.54****	**0.72*****	**0.57****	**0.74*****	**0.67*****	-0.21	**0.68*****
Environmental volume	**0.51***	**0.74*****	**0.65*****	**0.74*****	**0.73*****	-0.12	**0.68*****
Connectivity	**0.47***	0.14	-0.12	0.15	0.15	-0.03	0.31
Archipelago hull (m^2)	0.19	**0.55****	**0.64****	**0.49***	**0.62****	0.18	**0.43***
Proportion of land area	**0.46***	0.14	-0.11	0.16	0.13	-0.07	0.31

Table V.3.8. Coefficients and evaluation statistics for minimum adequate structural equation models (SEMs, A-D) of γ richness determinants. We tested biogeographic, climatic, and intra-archipelagic determinants as predictors of γ richness of vascular plants on 23 oceanic archipelagos worldwide. Explanatory variables are main axes (> 75% of explained variation) of separate principal component analyses (PCA) per variable category (see Fig. II.3.3c). See main text for the full model descriptions. Minimal adequate SEMs were obtained by stepwise exclusion of least significant variables and by evaluation of the Akaike Information Criterion (see Fig. V.3.2 for full models). At each step, we evaluated residual correlations, modification indices (mi), and model fits of the SEMs and used chi-square tests, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) as measures of model fit. We tested for spatial autocorrelation in residuals with Moran's I for multi-predictor least square regression models for each response variable, varying number of the neighbours (*k*) from 1 to 15. For significant Moran's I, we calculated simultaneous autoregressive (SAR) models. β_{rpl} = β replacement; β_{nst} = β nestedness; *Clim 1* = first axis of the climatic PCA; *Clim 2* = second axis of the climatic PCA; *Clim 3* = third axis of the climatic PCA; *BioGeo 1* = first axis of the biogeographic PCA; *BioGeo 2* = second axis of the biogeographic PCA; *IntraArch 1* = first axis of the intra-archipelagic PCA; *IntraArch 2* = second axis of the intra-archipelagic PCA. Significance: **.** $0.1>P>0.05$; * $0.05>P>0.01$; ** $0.01>P>0.001$; ***$P<0.001$.

SEM	**Variable**	**R^2 (%)**	**Predictor PCA axes**	**Estimate ± SD**	***P*-value**	**Standardized coefficient**	***P*-value (χ^2)**	**CFI**	**Lower 90% CI value of RMSEA**	**Checking residuals**	**Checking modification indices**	**Lowest Moran's I *P*-value; *k***	**SAR coefficient**
A	α	76	*BioGeo 2*	0.36±0.09	***	0.58	0.48	1	0	All values <1	Four mi values between 1 and 2.2	0.08; *k*=3	
			Clim 1	−0.22±0.06	**	−0.37							
			Clim 3	−0.37±0.08	***	−0.62							
			IntraArch 2	−0.14±0.05	**	−0.24							
	β_A	75	*BioGeo 2*	0.44±0.14	**	0.43						0.37; *k*=3	
			Clim 1	−0.25±0.11	*	−0.25							
			Clim 3	−0.50±0.14	***	−0.52							
			IntraArch 1	−0.38±0.08	***	−0.41							
	γ	99	*BioGeo 2*	0.06±0.02	**	0.08						0.61; *k*=12	
			Clim 1	0.04±0.01	**	0.06							
			Clim 3	−0.06±0.02	**	−0.08							
			α	0.47±0.04	***	0.39							
			β	0.47±0.02	***	0.62							
B	β_{rpl}	73	*BioGeo 2*	0.47±0.15	**	0.45	0.46	1	0	All values <1	Few values slightly above 1	0.26; *k*=1	
			Clim 3	−0.53±0.15	**	−0.54							
			IntraArch 1	−0.47±0.12	***	−0.50							
	β_{nst}	63	*BioGeo 2*	0.55±0.16	**	0.55						0.07; *k*=1	
			Clim 3	−0.48±0.17	**	−0.51							
			IntraArch 1	−0.39±0.14	***	−0.43							
	γ	98	*BioGeo 2*	0.15±0.04	***	0.20						0.003; *k*=5	0.16
			Clim 3	−0.13±0.04	**	−0.18							−0.14
			IntraArch 1	0.10±0.03	**	0.15							0.10
			IntraArch 2	−0.06±0.03	*	−0.08							−0.06
			β_{nst}	0.38±0.05	***	0.50							0.37
			β_{rpl}	0.34±0.06	***	0.46							0.32
C	β_A/ α	57	*IntraArch 1*	−1.32±0.24	***	−0.78	0.31	0.98	0	All values <1	Four mi values between 2 and 4	0.008; *k*=5	−1.34
	γ	83	*Clim 1*	−0.26±0.07	***	−0.32						0.11; *k*=1	
			Clim 3	−0.29±0.12	*	−0.39							
			BioGeo 1	0.24±0.10	*	0.31							
			BioGeo 2	0.31±0.10	**	0.40							
			β/α	0.11±0.04	**	0.27							
D	β_{rpl}/ β_{nst}	39	*BioGeo 1*	1.50±0.44	***	1.30	0.25	0.95	0	Two values between 1 and 1.26	Six mi values between 1 and 5	0.45; *k*=1	
			IntraArch 1	0.58±0.26	*	0.56							
			IntraArch 2	1.27±0.34	***	1.22							
	γ	72	*Clim 1*	−0.19±0.09	*	−0.25						0.16; *k*=4	
			Clim 3	−0.62±0.10	***	−0.86							
			BioGeo 2	0.53±0.11	***	0.69							

4. Supplementary information - Chapter II.4

Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern of fern diversity in the Southeast Asian archipelago

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Table V.4.1. Isolation metrics tested as predictors of regional fern diversity. Estimates and AIC values are derived from a linear regression model with habitat area and one isolation metric at a time as predictors of fern species diversity. Note that metrics quantifying the proportion of mountain area in the surrounding of the target mountain range increase with decreasing isolation. The metric chosen for the analyses is printed in bold. Of all metrics showing the expected negative relationship of isolation to diversity it has the lowest AIC value. Significance codes: * p< 0.05, ** p < 0.01.

Isolation metric		**Estimate**	**AIC**
Source landmass description	Area (km^2)/ Buffer (km)		
Distance to nearest mountain range (> 700 m a.s.l.) of certain minimum area	100	-0.19	150.4
	1000	-0.43	147.5
	10000	-0.23 *	144.6
	100000	0.08 *	142.5
	1000000	-0.02	150.2
Distance to nearest mountain range (> 700 m a.s.l.) of certain minimum area on a different island than the target mountain range	100	-0.22	150.2
	1000	0.09	150.3
	10000	0.31 *	144.4
	100000	0.08 *	142.5
	1000000	-0.02	150.2
Distance to nearest mountain range (> 700 m a.s.l.) of a least 100 km^2 on landmass of certain minimum area	100	-0.19	150.3
	1000	0.24	149.5
	10000	0.28 **	140.7
	100000	0.27 *	143.8
	750000	0.01	150.4
	1000000	**-0.15 ***	**142.6**
	10000000	0.00	150.5
Distance to nearest mountain range (> 700 m a.s.l.) of a least 100 km^2 on New Guinea	-	0.00	150.5
Proportion of mountain area (> 700 m a.s.l.) within a certain buffer distance in the surrounding of the target mountain range	10	-1817.78	149.3
	32	451.06	150.2
	100	1277.74	147.3
	316	2367.94	147.7
	1000	-7426.26 *	143.2
	3162	1332.25	148
Proportions combined: log10 (∑ proportion)	-	554.24	149.1

Table V.4.2. Explanatory variables used in the analysis of diversity along the island size gradient.

Explanatory variable
log Habitat area [km²]
Isolation [km]
Annual Mean Temperature [°C]
Mean Diurnal Range [°C]
Isothermality [°C]
Temperature Seasonality [°C]
Max Temperature of Warmest Month [°C]
Min Temperature of Coldest Month [°C]
Temperature Annual Range [°C]
Mean Temperature of Wettest Quarter [°C]
Mean Temperature of Driest Quarter [°C]
Mean Temperature of Warmest Quarter [°C]
Mean Temperature of Coldest Quarter [°C]
Annual Precipitation [mm]
Precipitation of Wettest Month [mm]
Precipitation of Driest Month [mm]
Precipitation Seasonality [mm]
Precipitation of Wettest Quarter [mm]
Precipitation of Driest Quarter [mm]
Precipitation of Warmest Quarter [mm]
Precipitation of Coldest Quarter
Bryophyte cover on trees [%]
Variation in Bryophyte cover on trees [%]
Mean Inclination [°]
Canopy cover [%]
Soil carbon content [mmol/g]
Soil nitrogen content [mmol/g]
Carbon/nitrogen ratio
Base saturation [%]
Nitrogen ion content [µmolc/g]
Aluminium ion content [µmolc/g]
Calcium ion content [µmolc/g]
Iron ion content [µmolc/g]
Kalium ion content [µmolc/g]
Magnesium ion content [µmolc/g]
Manganese ion content [µmolc/g]
Natrium ion content [µmolc/g]

Table V.4.3. Eigenvalues and cumulative proportion explained (cum. prop. expl. [%]) for variable reduction using Principal Components Analysis (PCA). Only axis used in the analysis are shown.

Variable set		**PC1**	**PC2**	**PC3**	**PC4**
Temperature local	eigenvalue	338800	-	-	-
(TEMP)	cum. prop. expl. [%])	0.73	-	-	-
Precipitation local	eigenvalue	32730	-	-	-
(PREC)	cum. prop. expl.[%])	0.90	-	-	-
Temperature regional	eigenvalue	35440	-	-	-
($\mathrm{TEMP}_{\mathrm{Reg}}$)	cum. prop. expl. [%])	0.95	-	-	-
Precipitation regional	eigenvalue	173700	73890	-	-
($\mathrm{PREC}_{\mathrm{Reg}}$)	cum. prop. expl. [%])	0.63	0.90	-	-
local environment	eigenvalue	5.264	4.0373	1.9853	-
(ENV)	cum. prop. expl.[%])	0.35	0.62	0.75	-

5. Supplementary information - Chapter II.5

Differences in species-area relationships across land plants: a macroecological perspective

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revised version with additional co-author Péter Sólymos published in *Global Ecology and Biogeography*, 2014, **23**, 1275-1283, DOI: 10.1111/geb.12230

Text V.5.1. References used to compile the species lists for each taxonomic group in Chapter II.5, including bryophytes (hornworts, liverworts, mosses; A), and pteridophytes and spermatophytes (B). The list for vascular plants are joined due to that in many instances the references provided data for both pteridophytes and spermatophytes.

A. References of data sources for bryophytes: Evans 1906; Evans 1911; Brotherus 1924; Crum & Miller 1956; Arnell 1957; Crum & Bartram 1958; Crum & Steere 1958; Flowers 1961; Haring 1961; Darlington 1964; Hässel de Menendez 1964; Iwatsuki & Sharp 1967; Crosby 1970; Imam & Ghabbour 1972; Boesen *et al.* 1975; Hong 1975; Bowers *et al.* 1976; Iwatsuki *et al.* 1976; Koppe 1976; El-Saadawi & Badawi 1977; Hong 1977a, b; Abeywickrama & Jansen 1978; Frisvoll 1978; Hong 1978; Bowers & Freckmann 1979; De Menéndez 1980; Ireland *et al.* 1981; Brassard 1982; Christy *et al.* 1982; Gradstein & Weber 1982; Brassard 1983; Crosby *et al.* 1983; Dewey 1983; Frisvoll 1983; Brassard 1984; Grolle & Piippo 1984a; Grolle & Piippo 1984b; Hollensen 1984; Belland 1985; Buck 1985; Dia *et al.* 1985; Bartlett 1986; Beever *et al.* 1986; Beever 1986; Hasegawa 1986; Dia *et al.* 1987; Ireland *et al.* 1987; Crum & Buck 1988; El-Oqlah *et al.* 1988; Afonina 1989; Bergstrom & Seppelt 1989; Elliott & Moore 1989; Gradstein 1989; Gradstein & Hekking 1989; Engel 1990; Florschütz-De Waard 1990; Koponen 1990; Dalton *et al.* 1991; Deguchi 1991a, b; Dia & Not 1991; Johansen 1991; De Sastre *et al.* 1993; Ando 1994; Churchill 1994; Delgadillo 1994; Frahm 1994; Ingerpuu *et al.* 1994; Iwatsuki 1994; Churchill & Linares C. 1995; Delgadillo *et al.* 1995; Düll 1995a, b; Beever *et al.* 1996; De Sastre & Santiago-Valentin 1996; Enroth 1996b, a; Frisvoll & Elvebakk 1996; Bai 1997; Duarte Bello 1997; Hong 1997; Kannukene *et al.* 1997; He 1998; Hong *et al.* 1998; Cogoni *et al.* 1999; Dauphin 1999; Churchill *et al.* 2000; Claudio 2000; Damsholt 2000; Delgadillo 2000; Futamura & Wheelwright 2000; Kürschner 2000; Abou-Salama & El-Saadawi 2001; Banu-

Fattah 2001; Erdağ *et al.* 2001; Hedderson *et al.* 2001; Joshi 2001; Karlin 2001; Akatova 2002; Blockeel *et al.* 2002; Cano *et al.* 2002; Grolle 2002b, a; Holz *et al.* 2002; Hong 2002; Ireland & Bellolio 2002; Abou-Salama & El-Saadawi 2003; Aleffi *et al.* 2003; Blockeel 2003; Higuchi & Nishimura 2003; Jóhannsson 2003; Kucera & Vána 2003; Akhani & Kürschner 2004; Cano *et al.* 2004; Chikovani & Svanidze 2004; Erzberger & Papp 2004; Heyn & Herrnstadt 2004; Aguirre-C. & Rangel-Ch. 2005; Ah-Peng & Bardat 2005; Cao *et al.* 2005; Churchill & Fuentes 2005; Cros *et al.* 2005; Dauphin 2005; Fuentes & Churchill 2005; Gabriel *et al.* 2005; Gradstein *et al.* 2005; Hebrard 2005; Ignatova *et al.* 2005; Kürschner & Erdag 2005; Banu-Fattah & Hadiuzzaman 2006a, b; Casas *et al.* 2006; Colacino & Sabovijevic 2006; Hallingbäck *et al.* 2006; Ho *et al.* 2006; Kürschner 2006; Bakalin & Cherdantseva 2007; Brinda *et al.* 2007; Cogoni *et al.* 2007; Eckel 2007; Aguirre-C. 2008; Ah-Peng *et al.* 2008; Celle 2008; Damsholt *et al.* 2008; Dulin 2008a, b; Engel *et al.* 2008; Frahm & Lüth 2008; Hastings 2008; Kellman 2008; Konstantinova & Savchenko 2008; Kürschner *et al.* 2008; Abay *et al.* 2009; Akiyama 2009; Bakalin *et al.* 2009; Casas *et al.* 2009; Churchill & Lozano 2009; Churchill *et al.* 2009a; Churchill *et al.* 2009b; Cogoni *et al.* 2009; De Menéndez & Rubies 2009; Fife & de Lange 2009; Frahm & Ho 2009; Haberle 2009; Hässel de Menéndez & Rubies 2009; Hedenäs *et al.* 2009; Ignatov *et al.* 2009; Jakovljev *et al.* 2009; Kannukene & Leis 2009; Konstantinova *et al.* 2009; Ah-Peng *et al.* 2010; Atwood & Davis 2010; Bakalin 2010; Daniels 2010; Davis & Pursell 2010; De Jesús *et al.* 2010; García-Fernández *et al.* 2010; Gradstein 2010; Harpel 2010; Hassel *et al.* 2010; Kürschner 2010; Alam *et al.* 2011; Bernarda & Schäfer-Verwimp 2011; Chuah-Petiot 2011; Costa *et al.* 2011; Dandotiya *et al.* 2011; Enroth & Shevock 2011; Garilleti *et al.* 2011; Higuchi 2011; Köckinger *et al.* 2011; Bruggeman-Nannenga & Wigginton 2012; Fuertes *et al.* 2012; Garcia *et al.* 2012; He 2012; Kirmaci *et al.* 2012; Gradstein & Ziemmeck 2013; Welch & Crum 1959; Wace & Dickson 1965; Pócs *et al.* 1967; Miller 1968; Schofield 1968, 1969; Lübenau & Lübenau 1970; Worley 1970; Worley & Iwatsuki 1970; McCleary & Green 1971; McCleary 1972; Schofield 1972; Pursell 1973; Schultze-Motel 1973; Vitt 1974; Robinson 1975; Whittier 1976; Mahler 1978; Miller *et al.* 1978; Steere & Brassard 1978; Steere & Inoue 1978; Schuster 1979; Steere & Scotter 1979; Vitt & Horton 1979; Mahler & Mahler 1980; Seppelt 1980a, b; Stark & Castetter 1982; Talbot & Ireland 1982; Miller *et al.* 1983; Matteri 1984; Matteri 1986; Lewinsky 1987; McKnight 1987; Menzel & Schultze-Motel 1987; Menzel & Shultze-Motel 1987; Schultze-Motel & Menzel 1987; Spence 1987; Tan *et al.* 1987; Whittier & Whittier 1987; Menzel 1988; Mohamed & Tan 1988; Schofield 1988; Snider *et al.* 1988; Schofield 1989; Long & Grolle 1990; Miller & Whittier 1990; Piippo 1990; Reese 1991; Moreno 1992; Touw 1992; Tan & Iwatsuki 1993; Weber 1993; Zetterstedt 1993; Lin *et al.* 1994; Long 1994; Onraedt 1994; Piippo 1994; Schofield *et al.* 1994; Orbán 1995; Redfearn & Tan 1996; Whittemore & Allen 1996; Zhang 1996; Piippo *et al.* 1997; Piippo & Koponen 1997; Rao *et al.* 1997; Reyes-Colón & Sastre 1998; Stotler *et al.* 1998; Townsend & Allen 1998;

Whittemore *et al.* 1998; Zhao 1998; Privitera & Puglisi 1999; Schäfer-Verwimp 1999; Shabbara 1999; O'shea 2000; Peng *et al.* 2000; Manville 2001; Sotiaux & Vanderpoorten 2001; Tsegmed 2001; Zhu & So 2001; Matteri & Schiavone 2002; O'shea 2002; Ochyra *et al.* 2002; Piippo *et al.* 2002; Streimann 2002; Streimann & Klazenga 2002; Suragina 2002; Suragina *et al.* 2002; Matteri 2003; Müller & Pursell 2003; Ochyra *et al.* 2003; Piippo & Koponen 2003; Sérgio & Carvalho 2003; Tan *et al.* 2003; Zhang & Corlett 2003; Zhu & So 2003; Matteri 2004; Mohamed *et al.* 2004; Norris & Shevock 2004a; Norris & Shevock 2004b; Papp 2004; Rykovsky & Maslovsky 2004b; Rykovsky & Maslovsky 2004a; Seppelt 2004; Staples *et al.* 2004; Uyar & Çetin 2004; Lagreca *et al.* 2005; Mogensen & Goldberg 2005; Nair *et al.* 2005; Natcheva & Ganeva 2005; Orrego 2005; Patiño & González-Mancebo 2005; Pócs & Ninh 2005; Siebel *et al.* 2005; Townsend 2005; Vana & Gremmen 2005; Yan *et al.* 2005; McCarthy 2006a; McCarthy 2006b; Muller 2006; O'Shea 2006; Sabovljević 2006; Sabovljević & Natcheva 2006; Seaward *et al.* 2006; Siebel *et al.* 2006; Smith 2006; Staples & Imada 2006; Suleiman *et al.* 2006; Szweykowski 2006; Vana & Gremmen 2006; Wigginton 2006; Yamada & Iwatsuki 2006; Zhao *et al.* 2006; Larraín 2007; Ledlie 2007; Müller & Pócs 2007; Park & Choi 2007; Pócs *et al.* 2007; Sérgio *et al.* 2007; Sotiaux *et al.* 2007; Weber & Wittmann 2007; Wigginton 2007; Lai *et al.* 2008; Manju *et al.* 2008; Medina *et al.* 2008; O'Shea & Price 2008; O'Shea 2008; Ochyra *et al.* 2008; Opisso & Churchill 2008; Pursell & Müller 2008; Ramírez P *et al.* 2008; Ramírez P. *et al.* 2008; Sabovljević *et al.* 2008; Sabovljevic *et al.* 2008; Sim-Sim *et al.* 2008; Malcolm *et al.* 2009; Manju *et al.* 2009; Müller 2009; O'Shea 2009; Rykovskij & Maslovskij 2009; Shevock & Buck 2009; Sotiaux *et al.* 2009; Tacchi *et al.* 2009; Wigginton 2009; Leblond *et al.* 2010; Losada-Lima *et al.* 2010; Motito Marín & Potrony Hechavarría 2010; O'Shea 2010; Privitera *et al.* 2010; Ros & Werner 2010; Schäfer-Verwimp 2010; Sim-Sim *et al.* 2010; Singh *et al.* 2010; Söderström *et al.* 2010; Thouvenot & Bardat 2010; Wigginton 2010; de Lange *et al.* 2011; Marka & Sabovljevic 2011; Müller *et al.* 2011; Pócs 2011; Sérgio & Garcia 2011; Söderström *et al.* 2011; Wang *et al.* 2011; Mifsud 2012; Singh & Barbhuiya 2012; Tefnu & Goia 2012; Vasco *et al.* 2012; Wigginton 2012; Puglisi *et al.* 2013a; Puglisi *et al.* 2013b; Söderström *et al.* 2013; Suárez & Schiavone 2013; Welch 2013; Ziemmeck & Harpel 2013.

B. References of data sources for pteridophytes and spermatophytes: Dahl 2004; Gauthier 1898; Tatewaki 1933; St John 1948; Glassman 1953; Lebrun 1960; Niering 1963; Wace & Dickson 1965; Calder & Taylor 1968; Ferro & Furnari 1968, 1970; Hansen 1972; Knapp 1973; Marchant 1973; Johnson & Simberloff 1974; Greene & Walton 1975; Johnson & Campbell 1975; Renvoize 1975; Brilli-Cattarini 1976; Lebrun 1976; Lorence 1976; St John 1977; Woodbury *et al.* 1977; Cronk 1980; Edwards 1980; Ozenda 1982; Boyland 1984; Frodin 1984; Neldner 1984; Davis *et al.* 1986; Le Houérou 1986; Fenghwai 1987; Lawesson *et al.* 1987; Bocchieri 1988; Major 1988; Manilal 1988; Myers 1988; Forero & Gentry 1989; Wang *et al.*

1989; Whitmore 1989; Kato 1990; Myers 1990; Tianwei 1990; Borhidi 1991; Stevanovic *et al.* 1991; Groombridge 1992; Thaman 1992; Whistler 1992; Hnatiuk 1993; Smith 1993; Tutin *et al.* 1993; Borkowsky 1994; Carazo-Motijano & Fernández-López 1994; Chas 1994; Davis *et al.* 1994; Green 1994b; Malyshev *et al.* 1994; Malyshev 1994; Sosa & Dávila 1994; Brullo *et al.* 1995; Davis *et al.* 1995; Felger & Wilson 1995; Florence *et al.* 1995; Gamisans & Jeanmonod 1995; Li 1995; Mateo Saenz & Crespo Villalba 1995; Samo Lumbreras 1995; Given 1996; Gustafsson & Ahlén 1996; Lowry II 1996; Rønning 1996; Sandbakk *et al.* 1996; Turner *et al.* 1996; Cronk 1997; Davis *et al.* 1997; Gabrielsen *et al.* 1997; Junak *et al.* 1997; Medail & Verlaque 1997; Morat & Lowry 1997; Takahashi *et al.* 1997; Chown *et al.* 1998; Hao & Yao 1998; Iverson & Prasad 1998; Marticorena *et al.* 1998; Martínez-Laborde 1998; Ono 1998; Segulja *et al.* 1998; Jørgensen & León-Yánez 1999; Ricketts *et al.* 1999; World Conservarion Monitoring Centre 1999; Barkalov 2000; Convey *et al.* 2000; Jiang & Zhang 2000; Pausas & Sáez 2000; Vangjeli & Ruci 2000; Frodin 2001; Hassler & Swale 2001; Martins 2001; McGlone *et al.* 2001; Tutin *et al.* 2001; van Wyk & Smith 2001; Broughton & McAdam 2002; Aldasoro *et al.* 2004; Meyer 2004; Roos *et al.* 2004; Bocchieri & Iiriti 2005; Borges *et al.* 2005; Broughton & McAdam 2005; MacMaster 2005; Meades *et al.* 2005; Wagner *et al.* 2005; Trusty *et al.* 2006; Florence *et al.* 2007; The Cook Islands Natural Heritage Trust 2007; UIB 2007; Borges *et al.* 2008; Arechavaleta *et al.* 2009; Chong *et al.* 2009; Nakamura *et al.* 2009; The Chinese Academy of Sciences 2009; Bowdoin Scientific Station 2011; Jaramillo Díaz & Guézou 2011; USDA 2011.

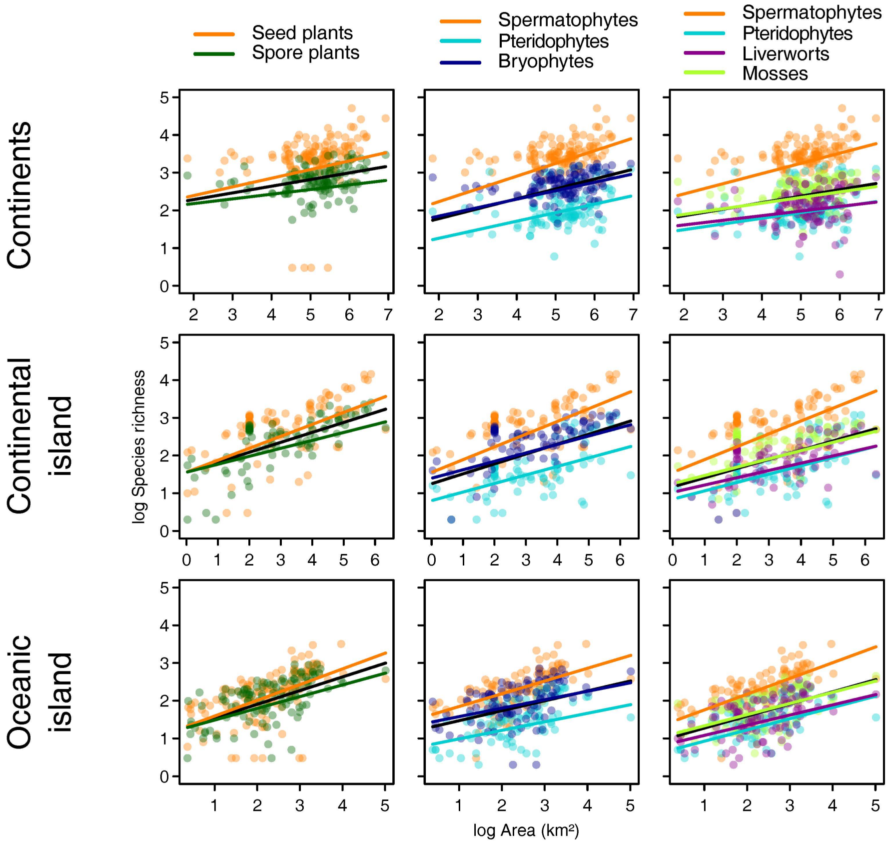

Figure V.5.1. Species-area relationships across land plants controlling for variation among taxonomic groups, geological settings, biomes, and realms. See Tables II.5.1 and II.5.2 for model description and parameter values. The response variable, species richness of each taxon group per geological system, was log-transformed and explained by island area (log-transformed, km^2).

Table V.5.1. Species richness ranges for each interaction of taxonomic group and geological setting.

	Continents	Continental islands	Oceanic islands
Spermatophytes	2 – 51,220	0 – 14,423	0 – 3,200
Pteridophytes	0 – 1,500	0 – 1,185	0 – 288
Bryophytes	26 – 1,731	1 – 1,359	1 – 716
Liverworts	1 – 842	0 – 623	0 – 361
Mosses	21 – 990	1 – 872	1 – 451

Table V.5.2. Coefficients of the power-law model describing variation in species richness in land plants depending on area size, controlling for variation among taxonomic groups (factor taxon: liverworts, mosses, pteridophytes, seed plants), geological settings (continental settings, continental islands, oceanic islands), biomes, and realms . Taxon groupings (Grouping), as follows: A = distinguishing seed- and spore-producing plants; B = spermatophytes, pteridophytes and bryophytes; C = spermatophytes, pteridophytes, liverworts and mosses. Liverworts include hornworts (see Methods in Chapter II.5). In bold, when *p*MCMC (*p* values estimated by the MCMC method using 10,000 simulations) was significant for the intercept and slope of area; HPDlower = lower boundary of the 95% highest posterior density interval; HPDupper = upper boundary of the 95% highest posterior density interval.

Fixed effects	Coefficient	HPDlower	HPDupper	*p*MCMC
Grouping A				
Intercept	**1.555**	0.746	2.412	**0.0242**
Slope	0.268	-0.484	1.034	0.3188
Grouping B				
Intercept	**1.237**	0.795	1.972	**0.0004**
Slope	0.262	-0.177	0.677	0.1698
Grouping C				
Intercept	**1.210**	0.737	1.804	**0.0006**
Slope	**0.245**	-0.038	0.563	**0.0412**

Table V.5.3. Coefficients (Coef) of the power-law model describing variation in species richness in land plants depending on area size controlling for variation among taxonomic groups (factor taxon: liverworts, mosses, pteridophytes, seed plants), biomes, and realms at the scale of continents, continental islands, and oceanic islands, respectively. Taxon groupings (Grouping), as follows: A = distinguishing seed- and spore-producing plants; B = spermatophytes, pteridophytes and bryophytes; C = spermatophytes, pteridophytes, mosses and liverworts. Liverworts include hornworts (see Methods in Chapter II.5). In bold, when *p*MCMC (*p* values estimated by the MCMC method using 10,000 simulations) was significant for the intercept and slope of area; HPD95lower = lower boundary of the 95% highest posterior density interval; HPD95upper = upper boundary of the 95% highest posterior density interval.

Fixed effects	Continent			Continental island			Oceanic island		
	Coef	HPDlower	HPDupper	Coef	HPDlower	HPDupper	Coef	HPDlower	HPDupper
Grouping A									
Intercept	**2.298**	**1.814**	**3.130**	**1.468**	**0.711**	**2.231**	**1.215**	**0.079**	**2.326**
Slope	**0.114**	-0.668	0.860	**0.292**	**-0.033**	**0.654**	0.350	-0.479	1.192
Grouping B									
Intercept	**2.191**	**1.709**	**2.605**	**1.349**	**0.843**	**1.824**	**1.052**	**0.623**	**1.469**
Slope	**0.111**	-0.046	0.288	**0.237**	**0.123**	**0.352**	**0.331**	**0.056**	**0.549**
Grouping C									
Intercept	**1.938**	**1.505**	**2.325**	**1.207**	**0.753**	**1.608**	**0.993**	**0.651**	**1.334**
Slope	**0.122**	**0.020**	**0.231**	**0.233**	**0.123**	**0.350**	**0.299**	**0.134**	**0.456**

Table V.5.4. Factors included in the random structure controlling for variation in the species-area relationships across land plants due to differences among taxonomic groups (factor taxon: liverworts, mosses, pteridophytes, and seed plants), geological setting (geology: continental islands, oceanic islands, continents) realms, and biomes. Models allowing or not for a varying intercept and all possible combinations of varying slopes for taxon, geology, realm, and biome. Only the best random effect structures (i.e. $\Delta AIC_c < 2$) are shown, as follows: in bold when $\Delta AIC_c = 0$; a 'blank field' indicates that the parameter was not included in a given model; taxon groupings (Grouping): 0 = distinguishing seed- and spore-producing plants; 1 = seed plants, pteridophytes and bryophytes; 2 = seed plants, pteridophytes, mosses and liverworts; liverworts include hornworts (see Methods in Chapter II.5).

	Intercept				Slope							
Taxon	**Geology**	**Realm**	**Biome**	**Taxon**	**Geology**	**Realm**	**Biome**	**AIC**	**AIC$_c$**	**ΔAIC**	**ΔAIC$_c$**	**Grouping**
	1	**1**	**1**	**1**	**1**	**1**	**1**	**699.3**	**699.7**	**0**	**0**	**0**
1	**1**	**1**	**1**	**1**	**1**	**1**		**872.1**	**872.3**	**0**	**0**	**1**
1		1	1	1		1	1	872.2	872.4	0.17	0.13	1
1	1	1	1	1		1	1	873.5	873.8	1.43	1.44	1
1	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1116.3**	**1116.5**	**0**	**0**	**2**

Table V.5.5. Factors included in the random structure controlling for variation in the species-area relationships in land plants due to differences in the geological setting (geology: continents, continental islands, and oceanic islands), realms, and biomes within each of five taxonomic groups (liverworts, mosses, pteridophytes, all spore producing plants, and seed plants). Models allowing or not for a varying intercept and all possible combinations of varying slopes for Geology, realm and biome. Only the best random effect structures (i.e. $\Delta AIC_c < 2$) are shown, as follows: in black bold when $\Delta AIC_c = 0$; a 'blank field' indicates that the parameter was not included in a given model. Liverworts include hornworts (see Methods in Chapter II.5).

Intercept			Slope							
Geology	**Realm**	**Biome**	**Geology**	**Realm**	**Biome**	**AIC**	**AIC$_c$**	**ΔAIC**	**ΔAIC$_c$**	**Taxon**
1	**1**	**1**	**1**	**1**	**1**	**284.2**	**284.7**	**0.00**	**0.00**	Seed plants
1		1	1	1	1	285.8	286.3	1.65	1.54	
	1	**1**	**1**	**1**	**1**	**295.3**	**295.7**	**0.10**	**0.00**	Spore-producing plants
1	1	1	1	1	1	295.1	295.7	0.00	0.01	
	1	**1**		**1**	**1**	**310.9**	**311.3**	**0.00**	**0.00**	Pteridophytes
		1		1	1	311.2	311.5	0.25	0.16	
		1	1	1	1	311.6	312.0	0.71	0.72	
	1	1	1	1	1	311.9	312.4	1.01	1.12	
	1	**1**	**1**	**1**		**339.4**	**339.7**	**0.00**	**0.00**	Liverworts
	1	1	1	1	1	341.2	341.6	1.82	1.92	
		1	**1**	**1**	**1**	**281.2**	**281.6**	**0.00**	**0.00**	Mosses
	1	1	1		1	281.5	281.9	0.28	0.28	
		1	1		1	282.2	282.5	0.98	0.89	
	1	1	1	1	1	282.1	282.5	0.81	0.91	
		1		1	1	283.0	283.2	1.73	1.64	
	1	1		1	1	283.0	283.3	1.73	1.73	
	1	1			1	283.3	283.6	2.05	1.96	

6. Supplementary information - Chapter II.6

Global patterns and drivers of phylogenetic assemblage structure in island plants

Patrick Weigelt, W. Daniel Kissling, Yael Kisel, Susanne A. Fritz, Dirk N. Karger, Michael Kessler, Samuli Lehtonen, Jens-Christian Svenning and Holger Kreft

Text V.6.1. Literature used to compile the global dataset of angiosperm, palm and fern species composition on 393 islands worldwide and description of taxonomic data treatment. The dataset includes 375 lists for all flowering plants (Angiospermae), 386 lists for palms (Arecaceae) and 328 for ferns (Moniliformopses). All species names (including subspecies and author information if available) were automatically matched to the working list of all known plant species (Plant List, www.theplantlist.org). Genus names not included in Plant List were carefully checked for mistakes and validity manually according to Mabberley's plant-book (Mabberley 2008). Within each genus, species were matched using fuzzy matching and replaced by names accepted by Plant List if necessary. If a name could not be matched or its taxonomic status in the Plant List was unresolved, we used the Taxonomic Name Resolution Service provided by iPlant (tnrs.iplantcollaborative.org) for taxonomic match-up. Species names matched but not resolved by either service or not found at all were used in their matched or original form (97.7% matched and 85.8% resolved for angiosperms, 97.2% matched and 65.3% resolved for ferns, 99.8% matched and resolved for palms; in total 95% using the Plant List, 5% using iPlant). All names entered further analyses at the species level. Family assignment followed Plant List which corresponds to the Angiosperm Phylogeny Group (APG) classification III (2009). To match the taxonomic concepts of the fern phylogeny and to acknowledge recent advances in fern taxonomy, all fern names were additionally subject to a comprehensive and careful taxonomic check so that genus and family assignments were up to date.

References used: Marquand 1901; Lester-Garland 1903; Christophersen 1931; Johnston 1931; Exell 1944; Fosberg 1949; Tatewaki 1957; Wace 1961; Sachet 1962; Egorova 1964; Wace & Dickson 1965; Sykes 1970; D'Arcy 1971; Chernyaeva 1973; Greene & Walton 1975; Johnson & Campbell 1975; Renvoize 1975; Esler 1978; Fosberg *et al.* 1980; Proctor 1980; Fosberg *et* *al.* 1982; Whistler 1983; Byrd 1984; Proctor 1985; Hill 1986; Fosberg & Sachet 1987; Kamari *et al.* 1988; Cronk 1989; Dowhan & Rozsa 1989; Levin & Moran 1989; Proctor 1989; Burton 1991; Du Puy 1993; Hnatiuk 1993; Telford 1993; Green 1994a; Stoddart & Fosberg 1994; Thaman *et al.* 1994; Iwatsuki *et al.* 1995; Jahn & Schönfelder 1995; Christodoulakis 1996; Moran 1996; Sandbakk *et al.* 1996; Whistler 1996; Gabrielsen *et al.* 1997; Junak *et al.* 1997; Parris & Latiff 1997; Takahashi *et al.* 1997; Alves 1998; Marticorena *et al.* 1998; Whistler 1998; Butler *et al.* 1999; de Lange & Cameron 1999; Takahashi *et al.* 1999; Ashmole & Ashmole 2000; Convey *et al.* 2000; McClatchey *et al.* 2000; Brofas *et al.* 2001; Case *et al.* 2002; Hill 2002; Takahashi *et al.* 2002; Wagner & Lorence 2002; Directorate of Wrangel Island Reserve 2003; Gerlach 2003; Kingston *et al.* 2003; McCrea 2003; Robinson *et al.* 2003; Stace *et al.* 2003; Miller & Morris 2004; Arechavaleta *et al.* 2005; Barker *et al.* 2005; Borges *et al.* 2005; Broughton & McAdam 2005; Conti *et al.* 2005; Kerguelen 2005; Wagner *et al.* 2005; Gage *et al.* 2006; Kelly 2006; Raulerson 2006; Searle & Madden 2006; Stalter & Lamont 2006; Takahashi *et al.* 2006; Taylor 2006; Acevedo-Rodríguez & Strong 2007; Athens *et al.* 2007; de Miranda Freitas 2007; Florence *et al.* 2007; UIB 2007; Borges *et al.* 2008; Franklin *et al.* 2008; Kristinsson 2008; Robinson *et al.* 2008; Wellington Botanical Society 2008; Arechavaleta *et al.* 2009; CARMABI 2009; Nakamura *et al.* 2009; Roux 2009; The Chinese Academy of Sciences 2009; Jackes 2010; Kirchner *et al.* 2010; Shaw *et al.* 2010; Baker & Duretto 2011; Bowdoin Scientific Station 2011; Jaramillo Díaz & Guézou 2011; Klotzenburg 2011; New Zealand Plant Conservation Network 2011; Kissling *et al.* 2012; Morat *et al.* 2012; University of Kent 2012; WCSP 2012.

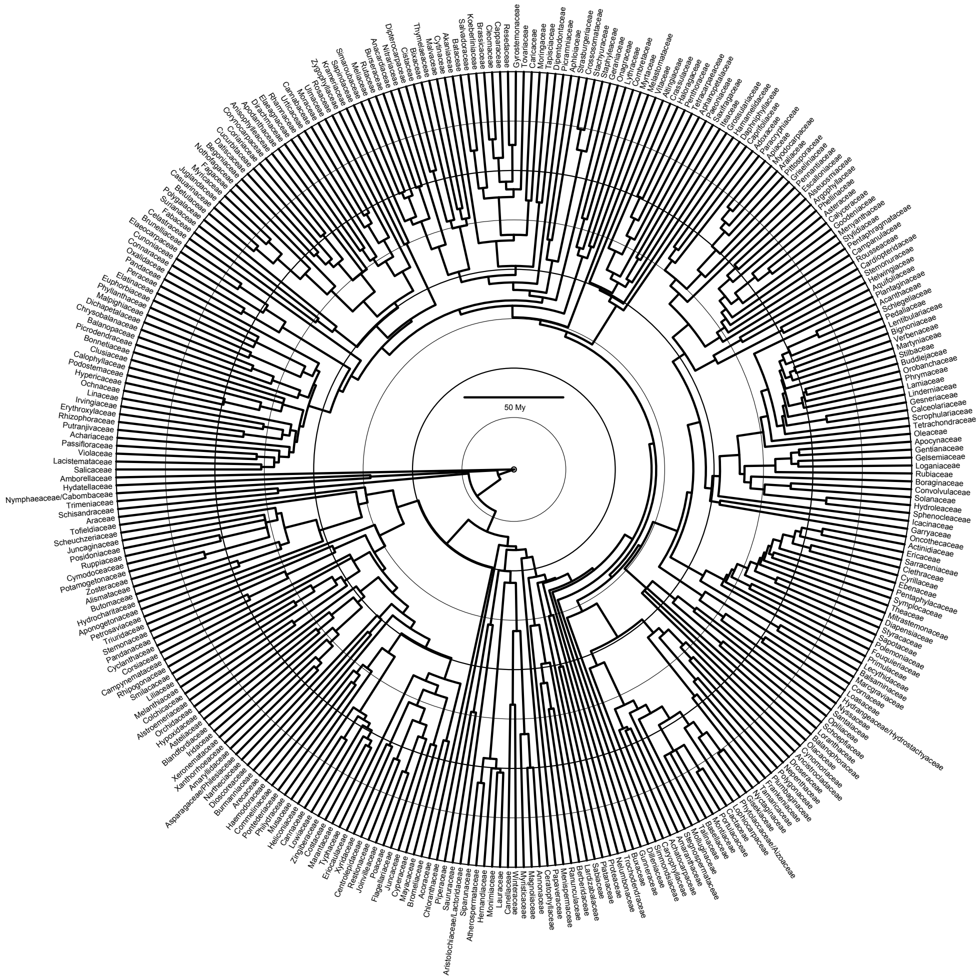

Figure V.6.1. Angiosperm phylogeny used for analyses on the phylogenetic assemblage structure of island floras. The original phylogeny (Bell *et al.* 2010) considered DNA sequence data of 560 angiosperm species from 335 families and 45 orders and was simultaneously estimated and dated using Bayesian methods based on 35 fossils and an additional age constraint for the root of the tree (Bell *et al.* 2010). For comparison with ferns, we pruned the phylogeny to family level. Five pairs of families that would otherwise not be monophyletic were merged (names at tree tips separated by slash). For the calculation of phylogenetic community metrics, the 32,446 angiosperm species from the island checklists were added to the family level phylogeny as polytomies at 1/3 of the family stem node ages (not shown here). Initially, 60 families representing 935 species were missing from the phylogeny and were manually added to the tree according to the phylogeny by Davies et al. (2004), the angiosperm phylogeny group (2009) classification III, and the angiosperm phylogeny website (Stevens 2001). In the cases of Achatocarpaceae, Alismataceae, Butomaceae, Cymodoceaceae, Juncaginaceae, Posidoniaceae, Potamogetonaceae, and Scheuchzeriaceae the position in the tree and ages relative to adjacent clades could be adopted from Davies et al. (2004). In all other cases, age estimates were not available (Anisophylleaceae, Aphanopetalaceae, Apodanthaceae, Balanophoraceae, Bonnetiaceae, Brunelliaceae, Calceolariaceae, Campynemataceae, Centrolepidaceae, Clusiaceae , Connaraceae, Corsiaceae, Cynomoriaceae, Cytinaceae, Dipentodontaceae, Dirachmaceae, Elatinaceae, Gisekiaceae, Gyrostemonaceae, Haemodoraceae, Hydatellaceae, Joinvilleaceae, Linderniaceae, Lophiocarpaceae, Loranthaceae, Mayacaceae, Mitrastemonaceae, Montiaceae, Nartheciaceae, Nitrariaceae, Nothofagaceae, Olacaceae, Pandaceae, Paracryphiaceae, Pennantiaceae, Pentaphragmataceae, Peraceae, Phrymaceae, Phyllanthaceae, Picramniaceae, Rhipogonaceae, Ruppiaceae, Salvadoraceae, Schlegeliaceae, Siparunaceae, Sphenocleaceae, Stegnospermataceae, Tetrachondraceae, Tovariaceae, Trimeniaceae, Triuridaceae, Xyridaceae). From these, families supposed to be the sister clade of a family in the tree were added at 2/3 stem age of the family in the tree. Families supposedly sister to larger clades were added half way between nodes. The final phylogeny pruned to only include species present in the considered island floras comprised 315 families and merged groups.

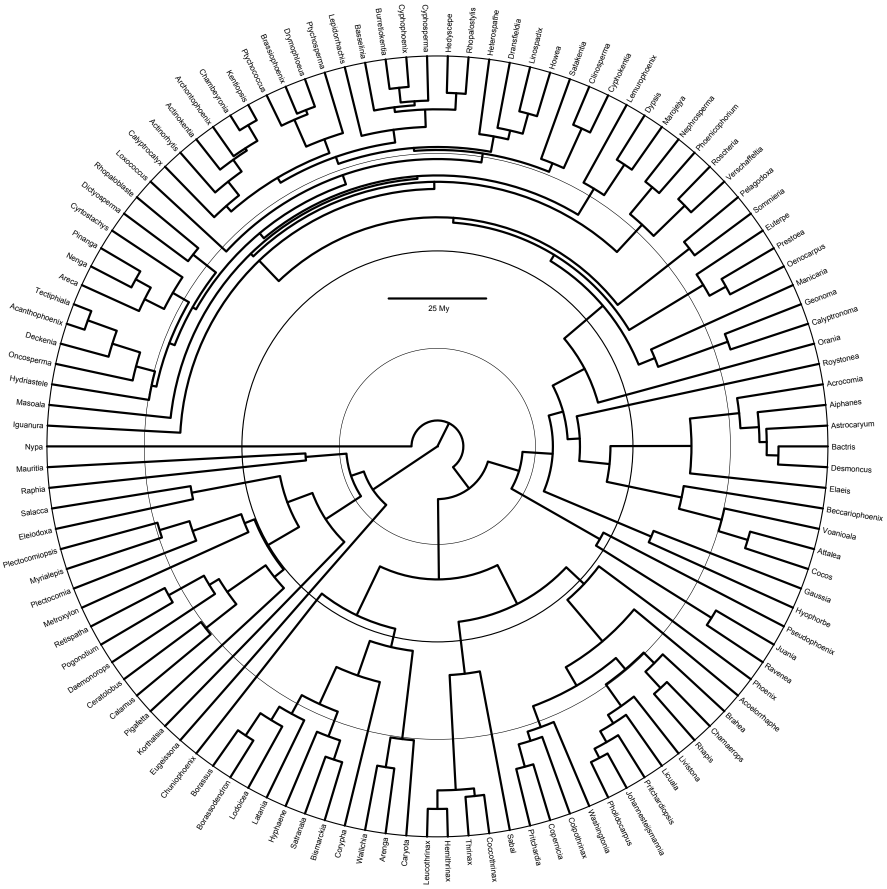

Figure V.6.2. Palm phylogeny used for analyses on the phylogenetic structure of island floras. The original phylogeny (Baker & Couvreur 2013) was based on a complete genus-level supertree of palms, dated using a Bayesian relaxed molecular clock approach with uncorrelated rates and calibrated using four palm fossil taxa and a stem node age constrained to 110 to 120 million year (Baker & Couvreur 2013). For comparison with ferns, we pruned the phylogeny to genus level. For the calculation of phylogenetic community metrics, the 1,143 palm species from the island checklists were added to the genus level phylogeny as polytomies at 2/3 of the genus stem node ages (not shown here; Kissling *et al.* 2012). All palm species included in the species checklists were represented by genera in the phylogeny. The final phylogeny pruned to only include species present in the considered island floras comprised 118 genera.

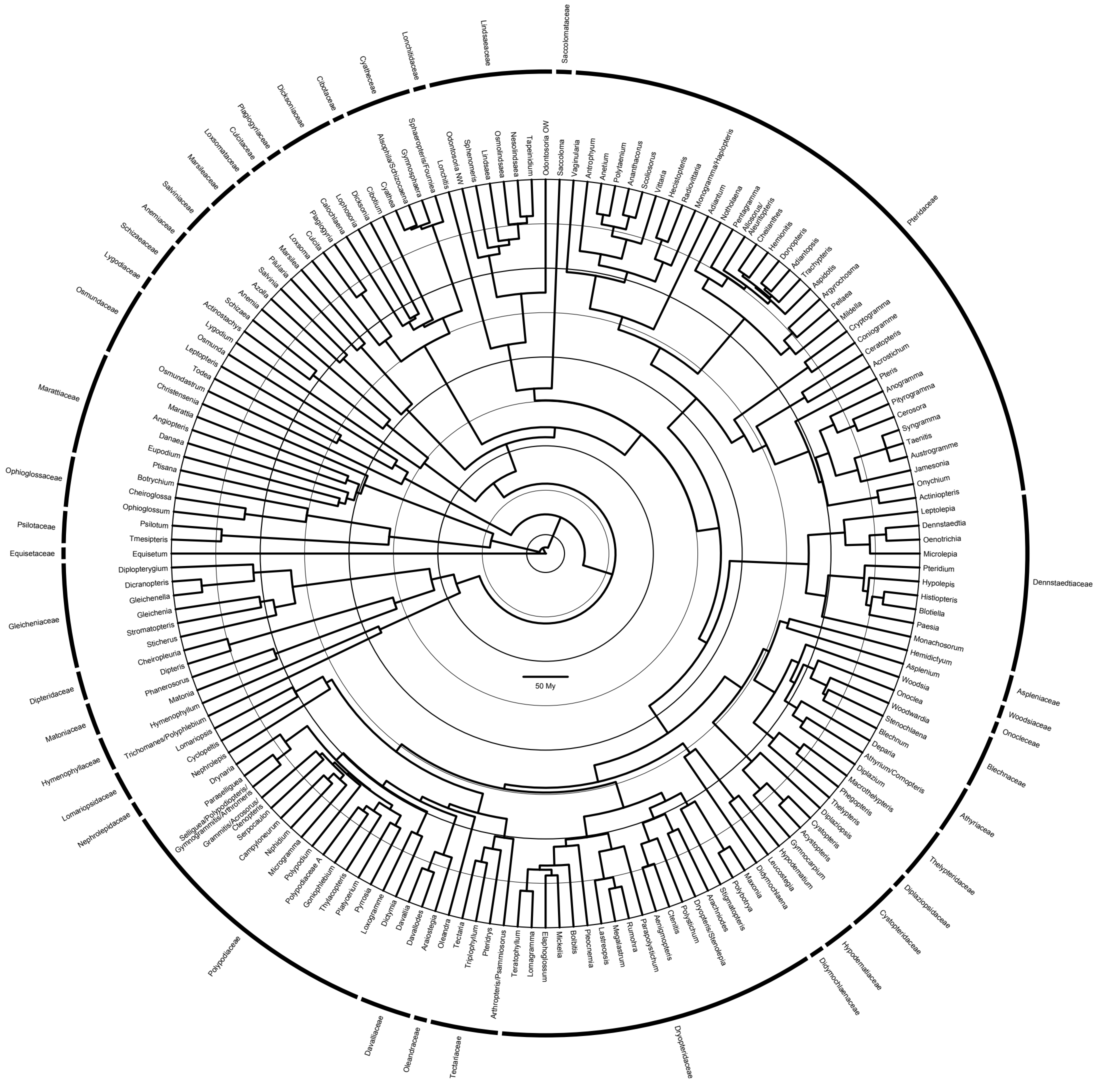

Figure V.6.3. Fern phylogeny used for analyses on the phylogenetic structure of island floras. The time-calibrated phylogeny was based on a global fern phylogeny dataset (Lehtonen 2011). This dataset was complemented with additional data and filtered to have a taxonomically broad sample of 1,118 well represented taxa including most extant fern genera. Molecular dating was based on uncorrelated exponential relaxed clock analysis in Beast 1.7.3 (Drummond *et al.* 2012), using 42 fossil calibrated nodes and a partially constrained starting tree produced in RAxML 7.3.0 (Stamatakis 2006; Ott *et al.* 2007). For comparison with angiosperms, we pruned the phylogeny to family level, and for comparison with palms, we pruned the phylogeny to genus level. The comparison between family- and genus-level analyses enabled us to investigate the sensitivity of our analyses to the resolution of the phylogenies. However, from a theoretical perspective, both levels provide enough detail to address the postulated hypotheses. Family-level phylogenies and even better the genus-level phylogenies with appended species polytomies serve well to disentangle patterns and determinants of phylogenetic community attributes of island floras since most variation in branch lengths is present in the higher-level parts of the phylogenies and higher resolution in the relationships among species would not considerably add to the overall patterns and dependencies. Dispersal-related traits and environmental adaptations are phylogenetically conserved in many large and old plant clades (Donoghue 2008), i.e. filtering mechanisms should clearly have profound implications on phylogenetic patterns at island assembly level using family- or genus-level phylogenies. Speciation in the form of island radiations happens fast and within small species groups or genera (Jønsson *et al.* 2012) leading to a suite of closely related species also if those species are appended to genus-level phylogenies as polytomies whereas relict lineages go back way beyond genus and even family level (e.g. Amborallaceae; Morat 1993). A group of nine genera in the fern phylogeny that would otherwise not be monophyletic was merged (Polypodiaceae A: *Lemmaphyllum*, *Lepidomicrosorium*, *Lepisorus*, *Leptochilus*, *Microsorum*, *Neocheiropteris*, *Neolepisorus*, *Paragramma*, and *Tricholepidium*). The genus *Odontosoria* was split into an old world clade (*Odontosoria* OW) and an new world clade (*Odontosoria* NW) to avoid a polyphyly. For the calculation of phylogenetic community metrics, the 3,689 fern species from the island checklists were added to the family level phylogenies as tips at 1/3 of the family stem node ages and to the genus level phylogenies as polytomies at 2/3 of the genus stem node ages. We chose 1/3 in the family phylogenies to account for the higher discrepancy between stem node ages of families and species when compared to genera and species in the genus-level phylogenies (2/3 stem node age). However, comprehensive sensitivity analyses of the palm phylogeny show that the specific age thresholds for polytomies do not qualitatively affect patterns and determinants of phylogenetic community structure (Kissling *et al.* 2012) because the metrics are predominantly influenced by long branch lengths in the older parts of the phylogenies. Initially, 25 genera representing 146 species were missing from the phylogeny and were placed manually to the tree according to literature information. Genera probably located inside genera in the tree were merged to the present genera (names at tree tips separated by slash). Genera supposed to be the sister clade of a genus in the tree were added at 2/3 stem age of the genus in the tree (*Aenigmopteris*, *Austrogramme*, *Cerosora*, *Cheiroglossa*, *Oenotrichia*, *Paraselliguea*, *Scoliosorus*, *Syngramma*, *Taenitis*, and *Vaginularia*). Genera supposedly sister to larger clades were added half way between nodes (*Ananthacorus* and *Trachypteris*). The genus *Adenoderris* had to be excluded due to an unknown phylogenetic position (one species with one occurrence on Jamaica). All fern species included in the species checklists were represented by families in the phylogeny. The final phylogeny pruned to only include species present in the considered island floras comprised 42 families and 168 genera.

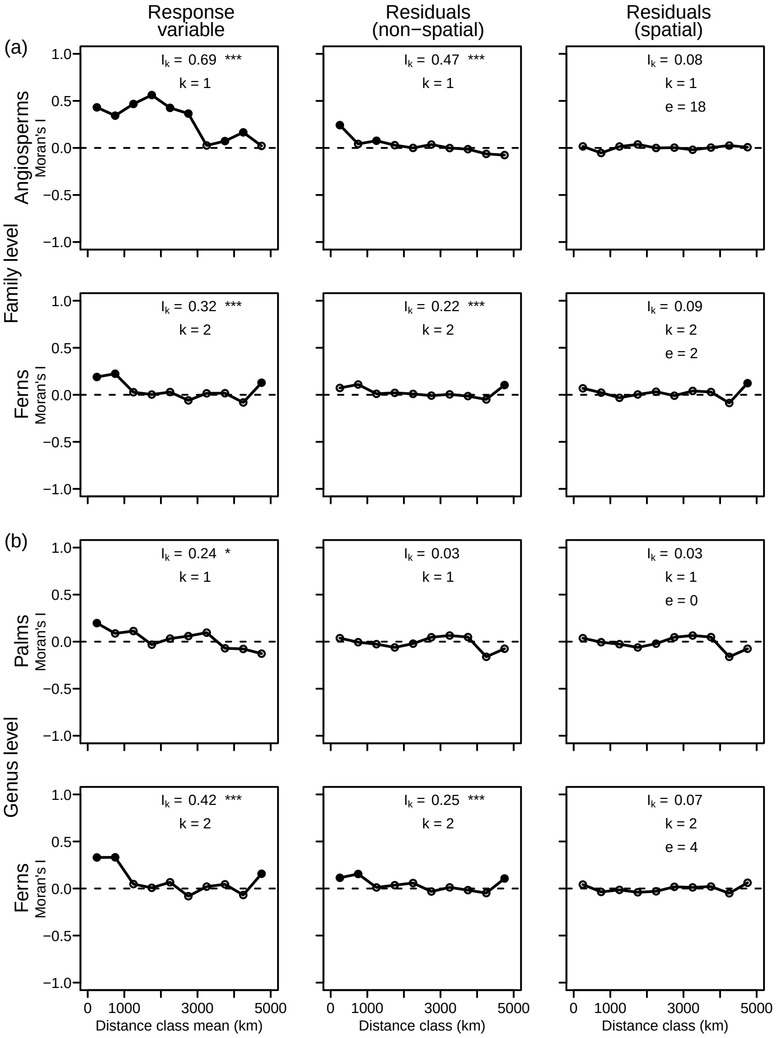

Figure V.6.4. Moran's I correlograms of spatial autocorrelation for the standardized effect size of phylogenetic diversity (PD_{es}; Response variable) of angiosperms, palms and ferns on islands; residuals from minimum adequate generalized additive models of PD_{es} in dependence on environmental predictors (Residuals (non-spatial)); and residuals from minimum adequate spatial models (Residuals (spatial)) including a set of *e* spatial eigenvectors to reduce spatial autocorrelation (Diniz-Filho *et al.* 2003). We applied principal coordinate analysis to a neighbourhood matrix (PCNM) to deconstruct geographic distances among island centroids into orthogonal spatial eigenvectors. Spatial distances were truncated by exchanging distances larger than 1,000 km by 4,000 km to put emphasis on small scale spatial autocorrelation (Diniz-Filho & Bini 2005). All eigenvectors with positive eigenvalues were considered as they represent positive spatial autocorrelation at different spatial scales. Following Griffith and Peres-Neto (2006), we consecutively added spatial filters to the minimum adequate models until residual spatial autocorrelation was not significant any more. In each round all possible models adding one spatial filter as linear effect were compared and the model with the lowest residual Moran's I value was retained for the next round. Moran's I values were calculated for varying neighbourhood structures considering the k = 1 to k = 25 nearest neighbours and always the highest significant Moran's I value was considered. Afterwards, the model selection procedure based on Akaike's information criterion corrected for small sampling sizes was repeated including the identified set of spatial eigenvectors in each model to find the minimum adequate spatial model. Residuals shown here were taken from those minimum adequate models. Only islands with at least two species of the focal group were included in models (n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns). In (a), PD_{es} was calculated based on dated family level phylogenies of angiosperms and ferns. In (b), PD_{es} was calculated based on dated genus level phylogenies of palms and ferns. Species were added to tree tips as polytomies. Moran's I values for the correlograms were calculated for ten distance classes of 500 km width each based on binary coded neighbourhood lists. Filled circles indicate spatial autocorrelation significant at $p < 0.05$ in contrast to non-significant autocorrelation (open circles). In addition we report Moran's I values based on row standardized neighbourhood lists of k neighbours per island (I_k). As used for the eigenvector selection we chose the highest Moran's I value out of values for k = 1 to k = 25. Significance of I_g: * $p < 0.05$, *** $p < 0.001$.

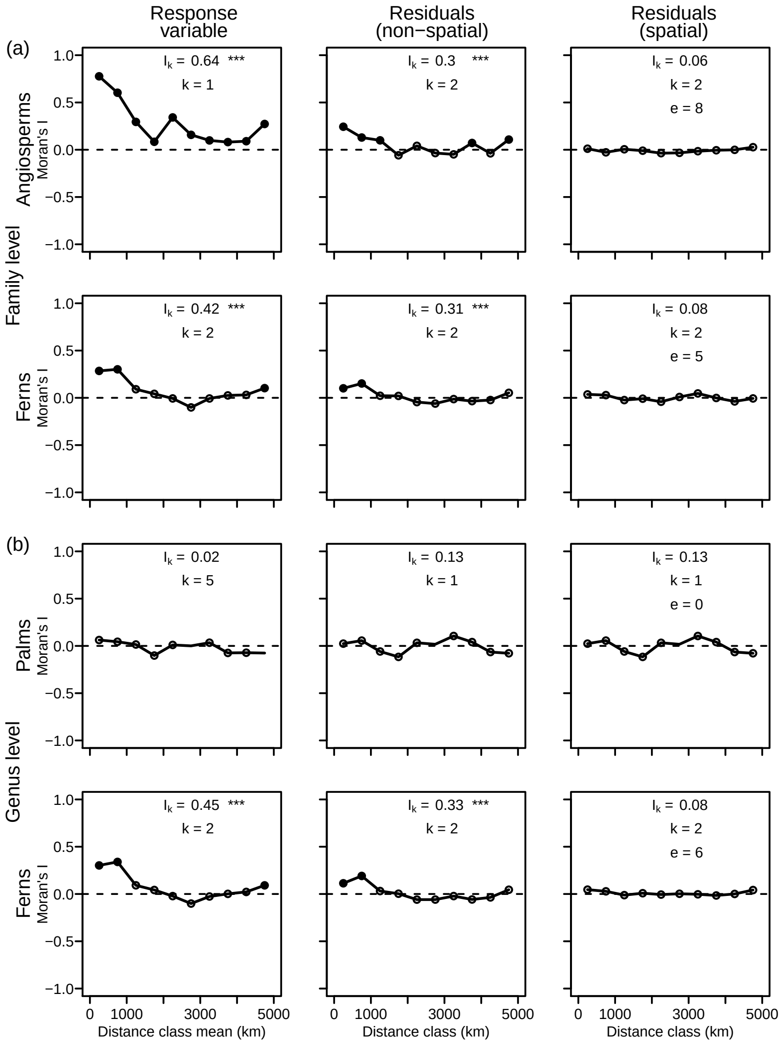

Figure V.6.5. Moran's I correlograms of spatial autocorrelation for the net relatedness index (NRI; Response variable) of angiosperms, palms and ferns on islands; residuals from minimum adequate generalized additive models of NRI in dependence on environmental predictors (Residuals (non-spatial)); and residuals from minimum adequate spatial models (Residuals (spatial)) including a set of *e* spatial eigenvectors to reduce spatial autocorrelation (see Fig. V.6.4 for details). Only islands with at least two species of the focal group were included in models (n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns). In (a), NRI was calculated based on dated family level phylogenies of angiosperms and ferns. In (b), NRI was calculated based on dated genus level phylogenies of palms and ferns. Species were added to tree tips as polytomies. Moran's I values for the correlograms were calculated for ten distance classes of 500 km width each based on binary coded neighbourhood lists. Filled circles indicate spatial autocorrelation significant at $p < 0.05$ in contrast to non-significant autocorrelation (open circles). In addition we report Moran's I values based on row standardized neighbourhood lists of k neighbours per island (I_k). We chose the highest Moran's I value out of values for k = 1 to k = 25. Significance of I_g: * $p < 0.05$, *** $p < 0.001$.

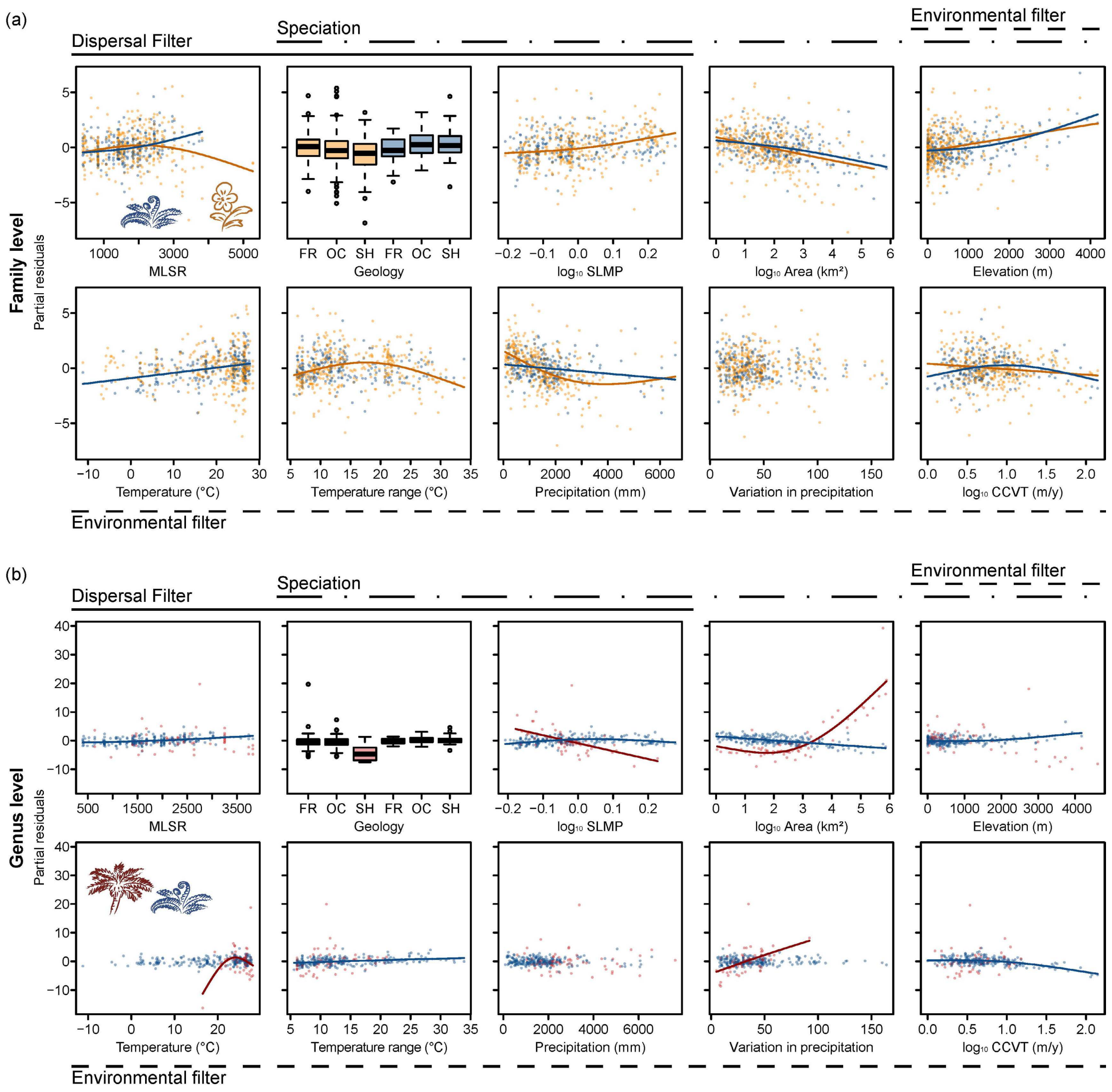

Figure V.6.6. Partial residual plots from averaged generalized additive models for the net relatedness index (NRI) of angiosperms, palms and ferns on islands in dependence on environmental predictors. Models also included spatial eigenvectors to account for spatial autocorrelation. Regression lines are only shown if the variable was significant in the averaged model. In (a), NRI was calculated based on dated family level phylogenies of angiosperms (orange) and ferns (blue). In (b), NRI was calculated based on dated genus level phylogenies of palms (red) and ferns (blue). Species were added to tree tips as polytomies. Only islands with at least two species of the focal group were included in models (n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns). Abbreviations follow Tables II.6.1 & V.6.4. Geologic island types: FR = continental fragment, OC = oceanic island (volcanic islands, atolls, uplifted sea floor), SH = continental shelf islands (mainly connected to the mainland during the last glacial maximum).

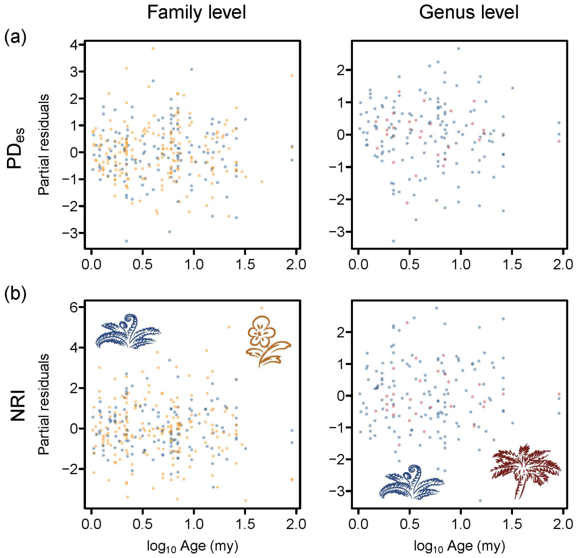

Figure V.6.7. Partial residual plots for island geologic age derived from averaged generalized additive models of (a) the standardized effect size of phylogenetic diversity (PD_{es}) and (b) the net relatedness index (NRI) of angiosperms, palms and ferns on islands. In addition to island age, the full model included a set of ten environmental predictors as well as spatial eigenvectors to account for spatial autocorrelation. The effect of island age was not significant in any averaged model ($p > 0.05$). Regression lines were therefore not plotted. PD_{es} and NRI were calculated based on a dated family level phylogeny for angiosperms (orange) and based on a dated genus level phylogeny for palms (red). For comparison with angiosperms, metrics for ferns (blue) were calculated based on a dated family level phylogeny (column 1) and for comparison with palms based on a dated genus level phylogeny (column 2). Only islands with at least two species of the focal group and with information on island age were included in models (n = 187 islands for all angiosperms, n = 31 islands for palms only and n = 138 islands for ferns).

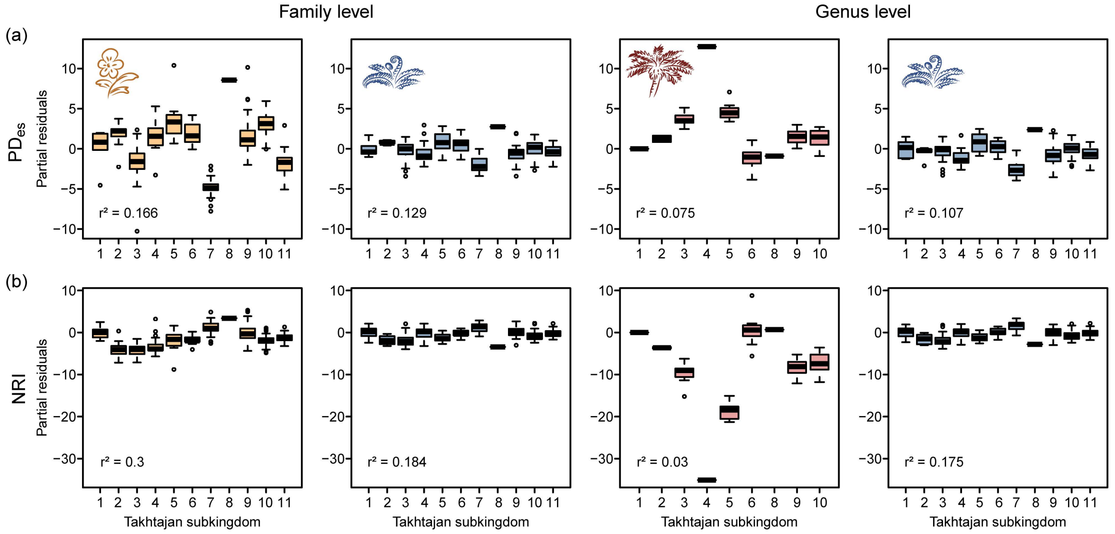

Figure V.6.8. Partial residual plots for Takhtajan's floristic subkingdoms derived from averaged generalized additive models of (a) the standardized effect size of phylogenetic diversity (PD_{es}) and (b) the net relatedness index (NRI) of angiosperms, palms and ferns on islands. In addition to Takhtajan's floristic subkingdoms, the full model included a set of ten environmental predictors as well as spatial eigenvectors to account for spatial autocorrelation. PD_{es} and NRI were calculated based on a dated family level phylogeny for angiosperms (orange) and based on a dated genus level phylogeny for palms (red). For comparison with angiosperms, metrics for ferns (blue) were calculated based on a dated family level phylogeny (column 2), and for comparison with palms, based on a dated genus level phylogeny (column 4). Takhtajan's floristic subkingdoms: 1 = African, 2 = Australian, 3 = Boreal, 4 = Holantarctic, 5 = Indomalesian, 6 = Madagascan, 7 = Madrean, 8 = Neocaledonian, 9 = Neotropical, 10 = Polynesian, 11 = Tethyan. Only islands with at least two species of the focal group were included in models (n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns).

Table V.6.1. Pearson correlations of phylogenetic community metrics among taxonomic vascular plant groups on islands worldwide. For angiosperms, metrics were calculated based on two dated family level phylogenies for comparison (Davies *et al.* 2004; Bell *et al.* 2010), for palms based on a dated genus level phylogeny. For comparison, metrics for ferns were calculated using phylogenies at family and genus level. NRI = net relatedness index, PD$_{\mathrm{es}}$ = standardized effect size of phylogenetic diversity (PD). n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns. Coefficients and significances were corrected for spatial autocorrelation following Dutilleul *et al.*(1993). Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Metric	**Taxon**	**Angiosperms**	**Angiosperms**	**Ferns (family)**	**Ferns (genus)**
PD	**Angiosperms (Bell *et al.*)**	1.00 ***			
	Ferns (family)	0.71 ***	0.71 ***		
	Ferns (genus)	0.71 ***	0.70 ***	1.00 ***	
	Palms	0.83 ***	0.83 ***	0.78 ***	0.78 ***
PD$_{\mathrm{es}}$	**Angiosperms (Bell *et al.*)**	0.98 ***			
	Ferns (family)	0.07	0.01		
	Ferns (genus)	-0.01	-0.07	0.91 ***	
	Palms	0.04	0.22	-0.27	-0.11
NRI	**Angiosperms (Bell *et al.*)**	0.99 ***			
	Ferns (family)	0.31 ***	0.30 **		
	Ferns (genus)	0.30 ***	0.29 **	0.99 ***	
	Palms	0.41 **	0.40 **	-0.28	-0.28

Table V.6.2. Pearson correlations of phylogenetic community metrics within taxonomic vascular plant groups on islands worldwide. For angiosperms, metrics were calculated based on a dated family level phylogeny, for palms based on a dated genus level phylogeny. For comparison, metrics for ferns were calculated using phylogenies at family and genus level. NRI = net relatedness index, PD$_{\mathrm{es}}$ = standardized effect size of phylogenetic diversity (PD). n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns. Coefficients and significances were corrected for spatial autocorrelation following Dutilleul et al. (1993). Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Taxon	**Metric**	**$\log_{10}$ SR**	**$\log_{10}$ PD**	**PD$_{\mathrm{es}}$**
Angiosperms	**$\log_{10}$ PD**	0.99 ***		
	PD$_{\mathrm{es}}$	-0.39 ***	-0.29 **	
	NRI	-0.04	-0.10	-0.56 **
Ferns (family)	**$\log_{10}$ PD**	0.96 ***		
	PD$_{\mathrm{es}}$	0.03	0.23 ***	
	NRI	-0.07	-0.24 ***	-0.86 ***
Palms	**$\log_{10}$ PD**	0.83 ***		
	PD$_{\mathrm{es}}$	-0.36 **	0.04	
	NRI	0.59 ***	0.32 **	-0.84 ***
Ferns (genus)	**$\log_{10}$ PD**	0.97 ***		
	PD$_{\mathrm{es}}$	-0.03	0.17 *	
	NRI	-0.05	-0.22 ***	-0.86 ***

Table V.6.3. Pearson correlations among predictor variables used to explain phylogenetic diversity patterns on 393 marine islands worldwide. Correlations with island age were calculated for a subset of n = 202 oceanic islands with information on the age of emergence. Abbreviations follow Tables II.6.1 & V.6.4. Note that Dist was not used in statistical models. Coefficients and significances were corrected for spatial autocorrelation following Dutilleul et al. (1993). Coefficients larger than 0.7 are printed in bold. Significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	MLSR	***Dist***	***SLMP***	***Area***	***Elev***	***Temp***	***varT***	***Prec***	***varP***	***CCVT***
Dist	-0.07									
SLMP	-0.10	**-0.73*****								
Area	0.04	-0.18*	0.08							
Elev	0.01	-0.06	0.00	**0.78*****						
Temp	0.55***	0.21	-0.24	-0.10	-0.07					
varT	-0.30*	-0.53*	**0.70*****	-0.02	-0.04	-0.55**				
Prec	0.22	0.31*	-0.43***	0.28***	0.43***	0.19	-0.29**			
varP	-0.07	-0.30	0.32*	-0.17*	-0.18*	0.31*	0.05	-0.48***		
CCVT	-0.22*	-0.22	0.34**	-0.48***	-0.48***	-0.43***	0.47***	-0.26**	-0.07	
Age	0.12	-0.09	0.12	0.14	-0.14	0.20*	-0.26***	-0.14	0.16*	-0.08

Table V.6.4. Variable importance estimated from all possible multi-predictor generalized additive models for phylogenetic clustering measured using the net relatedness index (NRI) for angiosperms, palms and ferns on islands. Importance was assessed as cumulative Akaike's information criterion corrected for small sampling sizes (AIC_c) weights of all models a variable was included. Apart from the variables shown here all candidate models included a set of spatial eigenvectors to account for spatial autocorrelation. For angiosperms, NRI was calculated based on a dated family level phylogeny, for palms based on a dated genus level phylogeny. For comparison, NRI of ferns was calculated using phylogenies at family and genus level. Columns Disp (dispersal filter), Spec (speciation), and Envi (environmental filter) indicate which hypothesized mechanism on NRI the variables relate to. Values larger than 0.9 are printed in bold.

Variable	**Abbr.**	**Disp**	**Spec**	**Envi**	**Angiosperms**	**Ferns (family)**	**Palms**	**Ferns**
Number of species in nearest mainland grid cell	***MLSR***	X			**0.93**	**1**	0.31	**1**
Geology (fragment, shelf, oceanic)	***Geol***	X	X		0.7	0.57	0.66	0.45
Surrounding landmass proportion ($\log_{10}$)	***SLMP***	X	X		**0.92**	0.72	**0.93**	**1**
Island area ($\log_{10}$; km^2)	***Area***		X		**1**	**0.97**	**1**	**1**
Elevational range (m)	***Elev***		X	X	**0.97**	**1**	0.86	**1**
Annual mean temperature (°C)	***Temp***			X	0.41	**0.95**	**0.95**	0.51
Temperature seasonality (range; °C)	***varT***			X	**0.99**	0.35	0.44	0.87
Annual precipitation (mm)	***Prec***			X	**1**	0.84	0.2	0.31
Precipitation seasonality (variation coefficient)	***varP***			X	0.31	0.42	**0.94**	0.25
Late Quaternary climate change velocity in temperature ($\log_{10}$; m/a)	***CCVT***			X	0.66	**0.94**	0.28	**1**

Table V.6.5. Minimum adequate generalized additive models based on Akaike's information criterion corrected for small sampling sizes (AIC$_c$) for the relationships of the standardized effect size of phylogenetic diversity (PD$_{es}$) of angiosperms, palms and ferns with environmental factors on islands. In addition to the parameters shown here, the models included sets of spatial eigenvectors to account for spatial autocorrelation. For angiosperms, PD$_{es}$ was calculated based on a dated family level phylogeny, for palms based on a dated genus level phylogeny. For comparison, PD$_{es}$ of ferns was calculated using phylogenies at family and genus level. Only islands with at least two species of the focal group were included in models (n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns). R^2 is a partial R^2 for the predictor variables, partialling out the effect of the spatial eigenvectors. Abbreviations follow Tables II.6.1 & V.6.4.

Term	Estimate	Std. error	edf	t/F-value	p-value	R^2
Angiosperms						0.49
Intercept	-4.185	0.092	1.000	-45.335	< 0.001	
Elev			1.507	2.328	0.104	
$\log_{10}$ *Area*			1.824	25.701	< 0.001	
MLSR			1.000	23.586	< 0.001	
Prec			1.933	37.997	< 0.001	
$\log_{10}$ *SLMP*			1.753	31.470	< 0.001	
Temp			2.000	23.428	< 0.001	
varP			1.000	4.408	0.037	
varT			1.853	32.879	< 0.001	
Ferns (family)						0.15
Intercept	0.253	0.072	1.000	3.518	0.001	
Elev			1.751	4.600	0.012	
$\log_{10}$ *Area*			1.000	5.536	0.019	
$\log_{10}$ *CCVT*			1.901	6.551	0.002	
MLSR			1.000	19.900	< 0.001	
Prec			1.775	8.257	< 0.001	
Palms						0.53
Intercept	-1.06	0.181	1.000	-5.864	< 0.001	
$\log_{10}$ *Area*			1.940	14.942	< 0.001	
MLSR			1.000	11.517	0.001	
$\log_{10}$ *SLMP*			1.000	16.075	< 0.001	
varP			1.592	8.394	0.001	
varT			1.952	8.078	0.001	
Ferns (genus)						0.18
Intercept	0.271	0.067	1.000	4.025	< 0.001	
Elev			1.859	5.521	0.005	
$\log_{10}$ *Area*			1.000	4.783	0.030	
MLSR			1.894	8.016	< 0.001	
Prec			1.000	9.083	0.003	
Temp			1.902	12.679	< 0.001	
varP			1.000	5.376	0.021	

Table V.6.6. Minimum adequate generalized additive models based on Akaike's information criterion corrected for small sampling sizes (AIC_c) for the relationships of the net relatedness index (NRI) of angiosperms, palms and ferns with environmental factors on islands. In addition to the parameters shown here, the models included sets of spatial eigenvectors to account for spatial autocorrelation. For angiosperms, NRI was calculated based on a dated family level phylogeny, for palms based on a dated genus level phylogeny. For comparison, NRI of ferns was calculated using phylogenies at family and genus level. Only islands with at least two species of the focal group were included in models (n = 363 islands for all angiosperms, n = 71 islands for palms only and n = 234 islands for ferns). R^2 was calculated as partial R^2 for the predictor variables, partialling out the effect of the spatial eigenvectors. Abbreviations follow Tables II.6.1 & V.6.4.

Term	Estimate	Std. error	edf	t/F-value	p-value	R^2
Angiosperms						0.37
Intercept	1.558	0.248	1.000	6.283	< 0.001	
Geol (oceanic)	-0.277	0.288	1.000	-0.964	0.336	
Geol (shelf)	-0.817	0.351	1.000	-2.324	0.021	
Elev			1.000	7.872	0.005	
$\log_{10}$ *Area*			1.000	17.833	< 0.001	
$\log_{10}$ *CCVT*			1.000	3.850	0.051	
MLSR			1.884	3.929	0.021	
Prec			1.935	18.375	< 0.001	
$\log_{10}$ *SLMP*			1.649	6.602	0.002	
varT			1.940	7.197	0.001	
Ferns (family)						0.25
Intercept	-1.029	0.235	1.000	-4.384	< 0.001	
Geol (oceanic)	0.612	0.280	1.000	2.183	0.030	
Geol (shelf)	0.536	0.322	1.000	1.667	0.097	
Elev			1.861	8.853	< 0.001	
$\log_{10}$ *Area*			1.417	6.327	0.005	
$\log_{10}$ *CCVT*			1.938	6.185	0.002	
MLSR			1.574	7.688	0.001	
Prec			1.000	6.032	0.015	
$\log_{10}$ *SLMP*			1.568	3.792	0.029	
Temp			1.000	13.937	< 0.001	
varP			1.000	2.041	0.155	
Palms						0.60
Intercept	3.073	0.782	1.000	3.930	< 0.001	
Geol (oceanic)	-0.371	1.142	1.000	-0.325	0.746	
Geol (shelf)	-4.897	1.859	1.000	-2.634	0.011	
Elev			1.710	4.938	0.012	
$\log_{10}$ *Area*			2.000	21.966	< 0.001	
$\log_{10}$ *SLMP*			1.000	7.181	0.009	
Temp			1.932	5.819	0.005	
varP			1.000	8.218	0.006	
Ferns (genus)						0.24
Intercept	-0.585	0.077	1.000	-7.553	< 0.001	
Elev			1.867	8.256	< 0.001	
$\log_{10}$ *Area*			1.000	36.435	< 0.001	
$\log_{10}$ *CCVT*			1.948	16.298	< 0.001	
MLSR			1.716	14.861	< 0.001	
$\log_{10}$ *SLMP*			1.940	9.415	< 0.001	
Temp			1.000	2.847	0.093	
varP			1.389	4.838	0.015	

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(legend top to bottom)

1 Mixed deciduous forest in the Hainich region (Central Germany)
2 Different insect taxa on the flowers of a thistle (*Cirsium* sp.)
3 *Glomeris* sp., a member of the decomposing soil fauna in forest ecosystems
4 *Pleodorina californica* (Chlorophyceae), colony-forming freshwater phytoplankton species
5 Grasshopper *Tettigonia cantans*, distributed from the Pyrenees to Northeastern China
6 *Microcebus berthae* (Cheirogaleidae), the smallest extant Primate species (Madagascar)
7 Tropical rain forest (Greater Daintree, Australia)
8 *Lethocolea glossophylla* (Acrobolbaceae), a liverwort of alpine mountain ranges in South America
9 Part of a coral reef in the Red Sea

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