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The macroecology of island floras

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Keywords:

Beta Diversity, Dispersal, Environment, Island Biogeography, Isolation, Phylogenetic Structure, Speciation, Species-Area Relationship

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Abstract:

Islands are key model systems in biogeography and ecology. However, standardized data on environmental characteristics of the large number of islands worldwide have so far been lacking, and the effects of these characteristics on island ecology and biodiversity remain insufficiently understood. In my PhD thesis, I presented the first comprehensive environmental characterization of the world's islands, covering past and present bioclimatic and physical island characteristics (including the spatial setting of islands and archipelagos). I used these data to investigate how island characteristics influence the diversity and assembly of island floras at different spatial scales and across major plant groups. To this end, I assembled a global database of vascular plant species composition including 45,000 species and covering 1,070 islands. I showed

that different aspects of island environments affect different facets of insular diversity (species richness, turnover, phylogenetic diversity) across scales and major plant groups, in accordance with their predominant dispersal- and speciation-related traits and adaptations to climate. The results contribute to a better understanding of the environmental and evolutionary drivers of plant assemblage composition, on islands as well as on mainlands.

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thesis abstract

The macroecology of island floras

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Abstract. Islands are key model systems in biogeography and ecology. However, standardized data on environmental characteristics of the large number of islands worldwide have so far been lacking, and the effects of these characteristics on island ecology and biodiversity remain insufficiently understood. In my PhD thesis, I presented the first comprehensive environmental characterization of the world's islands, covering past and present bioclimatic and physical island characteristics (including the spatial setting of islands and archipelagos). I used these data to investigate how island characteristics influence the diversity and assembly of island floras at different spatial scales and across major plant groups. To this end, I assembled a global database of vascular plant species composition including 45,000 species and covering 1,070 islands. I showed that different aspects of island environments affect different facets of insular diversity (species richness, turnover, phylogenetic diversity) across scales and major plant groups, in accordance with their predominant dispersal- and speciation-related traits and adaptations to climate. The results contribute to a better understanding of the environmental and evolutionary drivers of plant assemblage composition, on islands as well as on mainlands.

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Islands have intrigued biogeographers since the beginning of biogeographic research (e.g. Wallace 1880) and have inspired some of the most influential theories in ecology and evolution (e.g. MacArthur and Wilson 1967). Physical island characteristics, like their discrete boundaries and isolated nature, make islands excellent ecological model systems (Whittaker and Fernández-Palacios 2007). However, synthesis and comparative research in island biogeography have been hampered by the difficulties inherent in collecting standardized data on the world's thousands of (mostly very small) islands. Such data are crucial not only for advancing biodiversity research, but also for understanding and facing the increasing threats to island biodiversity like species invasions and climate change (Wetzel et al. 2013, van Kleunen et al. 2015). In my PhD thesis (Weigelt 2014), I therefore provided an environmental characterization of the world's islands and investigated how island characteristics relate to the diversity of island floras at the global scale. First, I focused on past and pre-

sent bioclimatic and physical island characteristics (with emphasis on the spatial setting of islands and archipelagos) as drivers of plant diversity; and second, I focused on taxon-specific, trait-related differences in the response of diversity patterns to abiotic factors.

In order to provide a rigorous and standardized bioclimatic and physical characterization of the world's islands (Weigelt et al. 2013), I calculated physical island characteristics using global coastline data¹ and digital elevation and bathymetry models (Hijmans et al. 2005, Amante and Ekins 2009) for 17,883 of the world's islands larger than 1 km². These characteristics were: area, distance to the nearest mainland, the land area as a proportion of total area of buffers (of 100, 1,000 and 10,000 km) surrounding the island perimeter (hereafter 'surrounding land area'), maximum elevation, and connection to mainland during the last glacial maximum (LGM). Furthermore, I calculated annual means and variability in temperature and precipitation using WorldClim data (Hijmans et al.

¹ GADM database of Global Administrative Areas, Version 1; www.gadm.org/version1/; last accessed 16 June 2010

2005) and climate change velocity in temperature since the LGM, i.e. the speed that a species has to move to keep up with climate change when considering topographic heterogeneity (Sandel et al. 2011). Using ordination and clustering techniques, I then characterized the world's islands in multidimensional environmental space. To showcase the usefulness of such a global data set, I made global predictions of insular vascular plant species richness. Species numbers for training the model were partly derived from a newly compiled and uniquely comprehensive database of 1,295 island plant checklists, including c. 45,000 native vascular plant species (Fig. 1). In contrast to existing datasets on island plant diversity, this is the first global one that includes actual species identities, enabling me to investigate species turnover among islands and phylogenetic diversity patterns at a global scale.

To address the roles of different aspects of island isolation in determining insular species richness I compared ecologically meaningful metrics of island isolation in models of vascular plant species richness (Weigelt and Kreft 2013). Despite the long-known, widely accepted importance of island isolation as a driver of immigration and speciation (MacArthur and Wilson 1967), the different facets of isolation – including stepping stones, surrounding landmass, wind and ocean currents, and climatic similarity between islands and mainlands – have only been addressed in a few case studies (e.g. Muñoz et al. 2004, Diver 2008). I therefore developed a set of 17 isolation metrics in 68 variations, calculated with accurate coastline data¹, and evaluated their explanatory power for vascular plant species richness for 451 islands worldwide. I hypothesized that the proportion of variation in species richness explained by isolation is higher when considering large source islands, stepping stones, climatic similarity, wind and ocean currents and the total area of surrounding landmasses, as opposed to considering only the commonly used metric of distance to the nearest mainland.

In addition to the degree of isolation of single islands, the spatial arrangement of islands within archipelagos should affect different aspects of diversity, such as the diversity of entire archipelagos (γ), the diversity of their constituent islands (α) or turno-

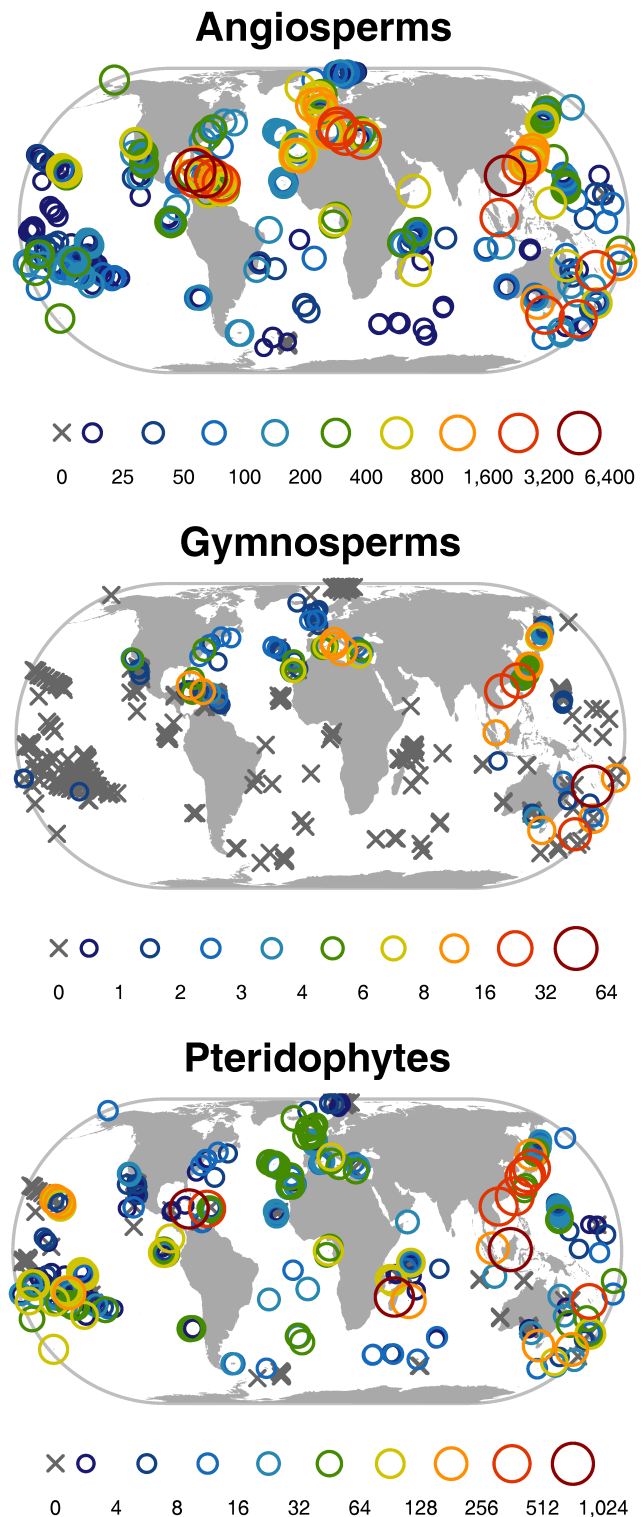


Figure 1. Species richness of native angiosperms ($n = 672$ islands), gymnosperms ($n = 666$) and pteridophytes ($n = 605$) on islands worldwide, derived from the global database of species checklists developed for my thesis. The database comprises 1,295 checklists for 1,070 islands or island groups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

ver among their islands (β) (Cabral et al. 2014). My colleagues and I investigated these three diversity components for the vascular plants on 23 archipelagos worldwide, and the extent to which they can be accounted for by biogeographic predictors (such as area, isolation and age), bioclimatic predictors and intra-archipelagic spatial predictors. We hypothesized that α is mainly driven by biogeographic and climatic determinants, that β is influenced mainly by the intra-archipelagic spatial structure, and that γ is mainly affected indirectly, i.e. through biogeographic, climatic and intra-archipelagic factors influencing α and β . We developed a set of predictors describing the intra-archipelagic spatial structure, including mean inter-island distance, connectivity, total archipelago area, range in island areas and the environmental volume occupied by an archipelago's islands as defined by the global bioclimatic and physical principal components analysis from Weigelt et al. (2013). We used multi-model inference to assess variables' importance in linear multi-predictor models, and structural equation models to test for the hypothesized indirect effects.

Island area, isolation and macroclimate are strong predictors of plant species richness at the island and archipelago level (MacArthur and Wilson 1967, Kreft et al. 2008), but it is unclear to what degree physical island characteristics predict species richness at a local, plot-level scale. My colleagues and I therefore tested whether area and isolation, the main physical island attributes considered by the equilibrium theory of island biogeography of MacArthur and Wilson (1967), can explain species richness at the plot level (Karger et al. 2014). We hypothesized that island area and isolation are important predictors of plant diversity only at large grain sizes and that their effects are diluted at small grain sizes (plot level) where local environmental conditions limit species diversity and communities may be saturated. We used field data on fern species richness in mountain forest plots on twelve islands in Indonesia and the Philippines (Karger 2013) to test for relationships between species richness and island area, isolation and macroclimate, as well as local environmental conditions, at grain sizes ranging from small plots to entire islands. For this analysis, we

used simple linear models and relative importance metrics.

Major groups of land plants differ in dispersal abilities and levels of gene flow, speciation rates and adaptations to climate (Donoghue 2008). Physical island characteristics may therefore affect different groups of organisms in different ways. To address this my colleagues and I tested whether major land plant groups differ in their species–area relationships (SAR) on islands and continental settings (Patiño et al. 2014). We expected that the geographic remoteness of oceanic islands would result in SARs with lower intercepts and a steeper slopes than SARs on continental islands, which would themselves have lower intercepts and steeper slopes than SARs of mainlands. We further hypothesized that SAR slopes and intercepts should increase from bryophytes to pteridophytes to spermatophytes because of decreasing dispersal abilities. We tested these hypotheses using a linear mixed-effects modelling approach, modelling variation in species richness as depending on area across geological systems and taxonomic groups.

To address how dispersal and environmental filtering in combination with *in-situ* speciation affect the composition of island assemblages, I again performed a cross-taxon comparison and studied phylogenetic structure of fern, angiosperm overall and palm assemblages (Weigelt et al. 2015). Traits related to dispersal, gene flow and adaptations to climate are often more similar among closely related species than expected by chance (Donoghue 2008). I therefore hypothesized that, when accounting for species richness, (a) phylogenetic diversity should decrease with environmental factors that increase chances of dispersal to islands; (b) phylogenetic diversity should be higher under environmental conditions that fit the bioclimatic requirements of more major lineages; and (c) phylogenetic diversity should decrease with factors increasing the probability of *in-situ* speciation on islands. I expected these relationships to be less pronounced for ferns than for angiosperms or palms (in particular) because ferns tend to have higher dispersal ability, wider distribution ranges and more frequent speciation through hybridization and polyploidization (Kessler 2010). Using generalized additive models, I investigated pat-

terns of phylogenetic diversity 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.

Results and Discussion

Altogether, my research shows how island characteristics (e.g. past and present climate or the spatial island setting) relate to different facets of insular diversity (species richness, turnover, phylogenetic assemblage structure) across scales (archipelago, island and plot-level) and major plant groups (e.g. bryophytes, ferns, seed and flowering plants).

The island characterization provides the first quantitative evidence that, globally, islands differ from mainland areas in their bioclimatic and physical characteristics (Weigelt et al. 2013). Islands are, on average, significantly cooler, wetter and less seasonal than mainlands. Because of their typically small size, they are less topographically heterogeneous. Wet temperate climates, which support temperate rainforests (one of the rarest ecosystems on Earth; Olson and Dinerstein 2002), are more prevalent on islands.

The new collection of physical island characteristics that I compiled, especially the quantification of island isolation and position relative to other islands and the mainland, allowed me and my colleagues to do thorough analyses of putative determinants of island plant diversity patterns. At the global scale, isolation was ranked as the second most important factor (after area) determining vascular plant species richness on islands (Weigelt and Kreft 2013). Using 'surrounding land area' as the isolation metric gained highest model support, suggesting that surrounding landmass is important as a source of constant recolonization ('rescue effect'; Brown and Kodric-Brown 1977). These results are in line with findings at smaller spatial extents (Diver 2008) and for habitat islands (Fahrig 2013). Also, the explanatory power of isolation for species richness increased when consid-

ering stepping stones, large islands as source landmasses and climatically similar source landmasses, compared with using the distance to the nearest mainland. I also showed that isolation was ranked as less important for large islands, where *in-situ* diversification is thought to counteract the negative effect of island isolation on immigration (compare Kisel and Barraclough 2010).

At archipelagic scales, aspects of intra-archipelagic spatial structure, particularly mean inter-island distance and range in island areas, were important in the models for β -diversity and, through β , for γ -diversity of vascular plants (Cabral et al. 2014). In the models, γ -diversity was mainly determined by indirect abiotic effects via α and β , with β being the more important component. These results suggest that mechanisms like *in-situ* diversification and island-hopping (Gillespie and Roderick 2002, Losos and Ricklefs 2009), which may drive patterns of β and γ -diversity on oceanic archipelagos, are linked to the intra-archipelagic spatial structure. These findings again highlight the importance for island biodiversity of physical island characteristics, in this case the location of islands relative to one another, and indicate the necessity of considering islands in an archipelagic context in island research.

However, the importance of physical island characteristics for diversity is thought to gradually decrease with spatial grain size (Karger et al. 2014). Consistent with island biogeography theory (MacArthur and Wilson 1967), my colleagues and I found strong correlations between fern species richness and both area and isolation only at the island level. In contrast, diversity at the plot level was mainly related to local environmental conditions. This is probably because local diversity is more saturated than diversity at large grain sizes, constraining the number of species from the species pool that can enter local communities (Fox and Srivastava 2006). To understand local diversity on islands, it is hence important to consider scale-dependent species pool effects (Karger et al. 2014).

The comparative cross-taxon analyses revealed clear differences among major plant groups in the correlations between putative envi-

ronmental drivers and both species richness and phylogenetic diversity (Patiño et al. 2014, Weigelt et al. 2015). As expected, my colleagues and I found an increase in SAR slopes from mainlands to continental islands to oceanic islands, and an increase in SAR slopes from bryophytes to pteridophytes to spermatophytes – though only for oceanic islands. Intercepts decreased from continents to continental islands to oceanic islands and from spermatophytes to bryophytes to pteridophytes (Patiño et al. 2014). These results challenge recent findings by Aranda et al. (2013), who found no differences in SARs among Macaronesian plant groups with varying dispersal ability and suggest that island assemblages of spore-producing plants are not always less species rich than continental assemblages (Patiño et al. 2015).

Furthermore, my models suggested that physical and bioclimatic island attributes, via their effects on environmental and dispersal filtering and speciation, determine the phylogenetic structure of island floras (Weigelt et al. 2015). Environmental predictors explained more variation in phylogenetic diversity and clustering for angiosperms and palms than for ferns, in accordance with expectations based on the high dispersal ability and large biogeographic ranges typical of ferns (Kessler 2010). When accounting for the effect of species richness on phylogenetic diversity, phylogenetic diversity was negatively related to isolation for palms but positively related for angiosperms, probably reflecting the immigration of angiosperm lineages from different biogeographic regions with distinct evolutionary histories to highly isolated islands. For both angiosperms and palms, phylogenetic diversity was negatively related to island area, suggesting an effect of *in-situ* speciation on large islands (Davies and Buckley 2011). However, in angiosperm assemblages mean-pairwise phylogenetic distances were also greater on large islands. This might be due to many angiosperm lineages with few or no speciation events and only a few large radiations on very large islands, which are mainly of continental origin (Weigelt et al. 2015).

Islands harbour large numbers of endemic species (Kier et al. 2009) and their biota

are threatened by habitat loss, biological invasions and changing climate (Kier et al. 2009, Wetzel et al. 2013, van Kleunen et al. 2015). The environmental characterization of the world's islands and the accompanying data and regionalizations presented in Weigelt et al. (2013) may serve as a spatial framework for macroecological research and conservation prioritization. My research demonstrates that accurate data on physical island characteristics are needed, for example 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 and Wilson 1967), ecologically meaningful descriptors of island isolation and intra-archipelagic structure have been lacking. The suite of metrics presented in my PhD research fills this gap and implies that a variety of colonization and inter-island migration mechanisms influence plant diversity patterns on islands and archipelagos at macro-scales (Weigelt and Kreft 2013, Cabral et al. 2014). The metrics should facilitate further research in island biogeography and could also be applied in related fields, such as research on habitat fragmentation (e.g. Fahrig 2013).

The database of island plant species' identities (Fig. 1) allows global analyses of patterns and putative drivers of biodiversity beyond species richness including β and phylogenetic diversity (Cabral et al. 2014, Weigelt et al. 2015). These facets of biodiversity have received increasing interest during the last few years (Beck et al. 2012) and are important for understanding the origin of global biodiversity patterns. Many relationships, such as the latitudinal beta diversity gradient and the relationship between functional and phylogenetic diversity, are still insufficiently understood (Fritz and Purvis 2010, Kraft et al. 2011, Tuomisto and Ruokolainen 2012). Islands may be key to answering some of the most compelling macroecological questions and the species database presented in my thesis, in combination with high-resolution phylogenies and information on species traits, will be supportive in this regard. As a start, I showed that relationships among environmental drivers and

species richness, as well as phylogenetic community attributes, vary among taxonomic groups in accordance with their predominant dispersal- and speciation-related characteristics (Patiño et al. 2014, Weigelt et al. 2015). This is a relatively new perspective in island biogeography and allows inferences about underlying processes affecting island diversity, such as dispersal, environmental filtering and speciation.

In conclusion, my research contributes to a better understanding of the composition of plant assemblages in relation to plant physiological constraints and the abiotic environment in general, on mainlands and 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. Islands may play a key role in achieving this goal.

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