



Dissecting global turnover in vascular plants

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ABSTRACT

Aim To provide a global assessment of turnover in vascular plants across geographical settings and taxonomic and functional groups. We tested whether turnover and its spatial and environmental drivers are affected by the geographical setting and whether taxonomic and functional groups exhibit specific turnover patterns that are associated with their ecological characteristics.

Location Global.

Methods We collated a global dataset of vascular plant checklists comprising 258 island and 346 mainland units. We created subsets based on the geographical setting of study units (mainland, islands, different island types) as well as taxonomic and functional properties of species (angiosperms, gymnosperms, pteridophytes, trees, shrubs, herbs). For the entire dataset, and each subset, the distance decay of similarity was assessed using generalized linear models. To disentangle the relative importance of spatial and environmental drivers of turnover, we employed generalized dissimilarity models. Finally, the model results were used to predict compositional similarity of vascular plants across a global grid.

Results The distance decay of similarity was stronger for mainland units than for islands. Among taxonomic and functional groups, the rate of decay was lowest for pteridophytes and highest for shrubs. Partitioning of turnover into distance- and environment-related effects revealed fundamental differences between mainland and island systems, with geographical distance being more important on the mainland than on islands. This trend was consistent across taxonomic and functional groups.

Main conclusions Our results reveal an important role of geographical context in shaping beta-diversity patterns. We argue that geographical settings are characterized by specific configurations of ecological filters that have a strong impact on the magnitude and structure of turnover. Moreover, taxonomic and functional groups are differentially successful in passing these filters, resulting in group- and setting-specific turnover patterns. Exploring these interdependences for different taxa and geographical settings at different scales will help to improve our understanding of beta diversity.

Keywords

Beta diversity, community assembly, dispersal filtering, distance decay, environmental filtering, functional groups, generalized dissimilarity modelling, island biogeography, taxonomic groups, variation partitioning.

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INTRODUCTION

Beta diversity, the variation in community composition among sites (Whittaker, 1960), is a central concept in ecology and biogeography as it provides a key link for understanding the relationships between species and their environment. Three main explanations for the origin of beta diversity have been proposed: (1) the uniformity hypothesis (Pitman *et al.*, 1999), stating that compositional variation arises as sampling artefact due to different local abundances of species; (2) the neutrality hypothesis (Hubbell, 2001), stating that compositional variation is created through stochastic, spatially limited dispersal, and speciation; and (3) the niche-assembly hypothesis (Whittaker, 1956; Hutchinson, 1957), stating that environmental factors determine the presence or absence of species and hence the compositional variation among sites. While the uniformity hypothesis predicts overall low beta diversity and has received little empirical support, numerous studies have contrasted the role of neutral versus niche-based processes (Condit *et al.*, 2002; Fargione *et al.*, 2003; Leibold & McPeck, 2006; Baldeck *et al.*, 2013). It is generally asserted that a strong spatial signal in community similarity indicates a strong role of dispersal limitation, thus supporting the neutrality hypothesis, whereas a strong environmental signal indicates strong habitat filtering, thus supporting the niche-assembly hypothesis (Legendre *et al.*, 2005). Importantly, these hypotheses are not mutually exclusive, and neutral and niche-based processes may act jointly in natural systems (Chase, 2014). The challenge in understanding beta diversity is therefore not to find a single universal explanation for all observable phenomena, but to evaluate the relative role of individual drivers and processes at different scales and in varying contexts.

Perhaps the most widely used approach to examine determinants of beta diversity is to track the change in compositional similarity along gradients of geographical or environmental separation. The rate at which compositional similarity decreases along such a gradient indicates the importance of the considered factor for species composition (Tuomisto *et al.*, 2003; Soininen *et al.*, 2007). Geographical distance is most frequently chosen as a predictor of compositional similarity (distance decay of similarity; Nekola & White, 1999) because it can be measured easily and ecological theory provides mechanistic explanations, e.g. spatially structured speciation or dispersal patterns (Hubbell, 2001), upon which testable hypotheses can be formulated. However, as Nekola & White (1999) pointed out, compositional and environmental similarity are both negatively correlated with geographical distance, making it difficult to disentangle the unique contributions of spatial and environmental factors to beta diversity. Moreover, and unlike geographical distance, there is no canonical measure of environmental distance because relevant target variables are both scale and taxon dependent and differ in their relative importance. Several methods have been proposed to address these issues, including multiple regression on distance matrices (Manly, 1986),

variation partitioning (Borcard *et al.*, 1992) and generalized dissimilarity modelling (Ferrier *et al.*, 2007).

The diverse approaches to analysing beta diversity are often applied to different subsets such as taxonomic groups (Tuomisto *et al.*, 2003; Ruokolainen *et al.*, 2007), functional groups (Bin *et al.*, 2010; López-Martínez *et al.*, 2013) or geographical settings (Fattorini, 2010; Stuart *et al.*, 2012), where each subset serves as an independent test case under different conditions. Comparing species groups with differential dispersal abilities, for example, allows one to infer about the strength of dispersal-related (distance dependent) determinants of beta diversity. Contrasting geographical settings with distinct properties, on the other hand, may yield insights into the relative importance of assembly processes under different environmental conditions. However, there are very few studies on beta diversity that take advantage of species-level traits as well as environmental factors.

Here, we present a global analysis of vascular plant beta diversity using a large floristic dataset of 604 checklists comprising 149,475 species. We focused on the turnover (i.e. richness insensitive) component of beta diversity and examined different geographical, taxonomic and functional subsets in order to identify the factors determining turnover at global scales. To assess the general strength of turnover, we analysed the distance decay of similarity in each subset. We then applied generalized dissimilarity models with an additional set of environmental predictors to disentangle the relative importance of spatial and environmental drivers, and to predict floristic similarity across a global equal-area grid. We hypothesize that turnover and the importance of spatial and environmental variables vary: (1) across geographical settings, indicating that different geographical settings impose distinctive combinations of dispersal and environmental filters, and (2) across taxonomic and functional groups, indicating that groups are differentially successful in passing these filters. In particular, we expect geographical distance (i.e. dispersal filtering) to be the predominant driver in island systems and environmental conditions (i.e. environmental filtering) to be predominant drivers in mainland systems. On the other hand, we expect groups with, on average, good dispersal abilities to be less sensitive to geographical distance. Likewise, groups composed of species with large environmental tolerances should be less sensitive to environmental distances.

METHODS

Species data

Building on previous work of Weigelt *et al.* (2015), we assembled vascular plant checklists from published floras, checklists and online databases (data sources are listed in the Appendix). We standardized species names and higher taxonomic ranks according to The Plant List (2013) and, for species not listed in The Plant List, we used iPlant's taxonomic name resolution service (Boyle *et al.*, 2013). Our inclusion criteria for checklists were that: (1) the checklist was sufficiently complete, i.e. the number of reported species fell into

a reasonable range for the given biome and area (Kreft & Jetz, 2007), (2) the floristic status (native versus alien) of all species was documented, (3) the checklist contained more than 30 native vascular plant species to allow robust statistical analyses, and (4) the corresponding geographical unit could be clearly defined and had a size between 1 and 500,000 km². To increase comparability among and environmental consistency within operational geographical units (hereafter OGUs), we focused on collecting mainland checklists for relatively small regions such as protected areas or federal states. The final dataset consisted of 258 island and 346 mainland OGUs containing a total of 149,475 native plant species (all alien species were excluded) and 771,403 species records (see Appendix S1 in Supporting Information).

We collected morphology-related trait information from the original checklists and additionally from the following large databases: TROPICOS (Missouri Botanical Garden, 2015), USDA PLANTS (USDA & NRCS, 2015), World Checklist of Selected Plant Families (WCSP, 2014), TRY (Kattge *et al.*, 2011), CanadenSys (Desmet & Brouillet, 2013) and Useful Tropical Plants (Fern & Fern, 2015). Since the terminology for trait information differed greatly across resources, we translated the original descriptions into a hierarchical system of growth-form and life-form traits with defined values for each level (Appendix S2). We then used values from highly resolved levels to deduce missing values for coarser levels. Where resources provided conflicting trait values for a given species (less than 5% of cases), we used a threshold of at least 66% agreement to finally assign a value to the species. Although more detailed traits, such as life-form *sensu* Raunkiaer (1934), are ecologically more informative, we chose growth form (values: herb, shrub and tree) as the target variable in all trait-related analyses because it represented the best compromise between data coverage and ecological relevance. In this way we could assign growth-forms to a total 102,809 out of 149,475 species and achieved an average coverage of 81.9% and 87.1% for island and mainland OGUs, respectively.

Abiotic data

Spatial polygons for OGUs were assembled from the GADM database of Global Administrative Areas (Hijmans *et al.*, 2009) for political units and islands and from the World Database of Protected Areas (IUCN and UNEP-WCMC, 2014) for protected areas. Some OGUs were digitized manually on the basis of information given in the respective publication (maps, coordinates). The geographical distance between OGUs was calculated as the distance between the polygon mass centroids on a sphere with the earth's radius. Environmental data were extracted from 30 arcsec WorldClim raster layers (Hijmans *et al.*, 2005) for annual mean temperature, annual mean precipitation, temperature seasonality, precipitation seasonality and elevation. These variables have been shown to capture major ecologically relevant axes of environmental space (Moser *et al.*, 2005; Kreft & Jetz, 2007; Weigelt & Kreft, 2013). Because of the skewed

distribution of raster cell values, we did not use the means but the medians of all cells overlapping with an OGU as environmental predictors. Pairwise correlation plots and variance inflation factors did not indicate problematic levels of multicollinearity among the predictor variables (Appendix S3). Island geology, distinguishing between continental islands (i.e. shelf islands and continental fragments), oceanic islands (i.e. islands of volcanic origin or uplifted by tectonic processes) and atolls (i.e. flat, ring-shaped coral islands) were ascertained through extensive literature research.

Compositional similarity

Beta diversity describes two independent sources of compositional variation: the replacement or *turnover* component, reflecting the amount of change in species identities among study sites, and the *nestedness* component, reflecting the compositional variation owing to differences in species numbers (Lennon *et al.*, 2001; Baselga, 2010; Legendre, 2014). We quantified compositional variation using the β_{sim} index which is insensitive to richness differences and thus only quantifies the turnover component of beta diversity (Baselga, 2010). This is a crucial property when comparing units of unequal area, as we do here, because of the strong dependence of species number on area (Arrhenius, 1921; Connor & McCoy, 1979). The index is defined as $\beta_{sim} = \min(b,c)/(\min(b,c) + a)$ where a is the number of species common to both comparison units and b and c are the number of species unique to the first and second unit, respectively.

We calculated a binary species-by-sites matrix containing all species and all OGUs. Based on geographical, taxonomic and functional criteria, we produced different subsets of the full matrix (Fig. 1). We derived row-wise subsets for mainland units, islands and particular island types as well as column-wise subsets for angiosperms, gymnosperms, pteridophytes, trees, shrubs and herbs. We also produced separate island- and mainland subsets for all taxonomic and functional groups. For each subset, we computed separate β_{sim} similarity matrices. If an OGU had fewer than 10 species of a particular taxonomic or functional subset, it was excluded from the respective similarity matrix to avoid bias emerging from low sample size. Moreover, we excluded OGUs from the functional subsets when the growth form was known for fewer than 80% of the species.

Analysis

Turnover was assessed in a two-step approach (Fig. 1). First, we were interested in the general pattern of turnover for the different geographical, taxonomic and functional subsets and applied single-predictor log-binomial generalized linear models (GLMs), producing a best-fit decay curve of compositional similarity against geographical distance. The intercept was fixed at 1, assuming complete similarity at a distance of 0 km. Following Soininen *et al.* (2007), we used the *halving distance* ($D_{S/2}$), i.e. the distance after which a given similarity value is predicted to decrease by 50%, as a measure of the

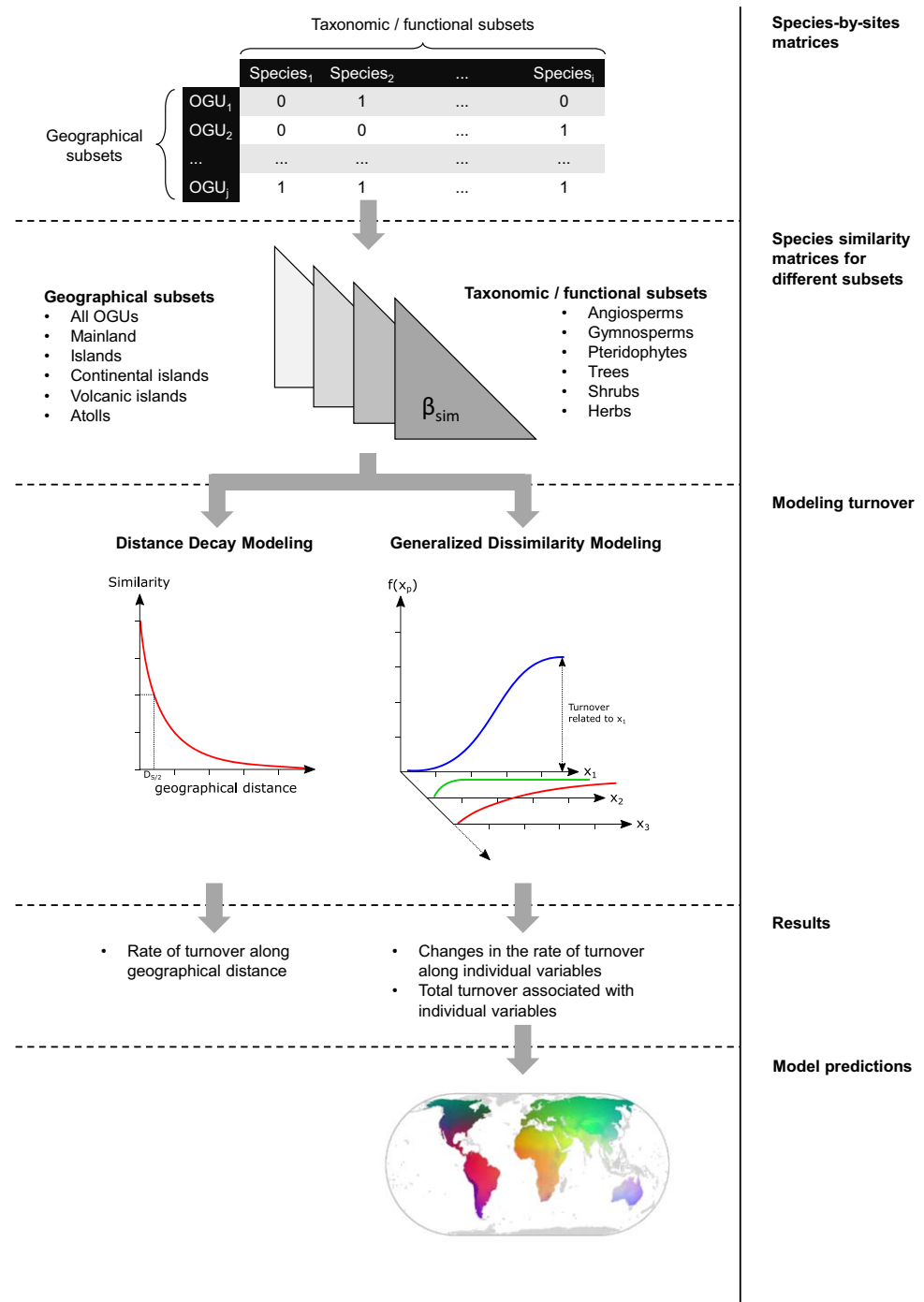


Figure 1 Framework of this study for analysing global turnover of vascular plants. Subsets of the species-by-sites matrix were produced on the basis of geographical, taxonomic and functional criteria. For each subset, turnover along geographical and environmental gradients was assessed using single predictor log-binomial generalized linear models and multi-predictor generalized dissimilarity models (GDM). Abbreviations: $D_{S/2}$, distance after which similarity decreases by 50% (halving distance); $x_1 \dots x_p$, GDM predictor variables; $f(x_1 \dots x_p)$, GDM transformation functions for $x_1 \dots x_p$ that maximize the deviance explained by full model; OGU, operational geographical unit.

turnover rate. Due to the constant rate of decay assumed in the model, the halving distance holds as a descriptor of turnover per unit distance over the whole gradient. Acknowledging that the non-independence of observations in similarity matrices leads to correct parameter estimates but invalid test statistics (Lichstein, 2007), we estimated confidence intervals for the GLMs using a bootstrapping approach. We randomly excluded 50% of OGUs from each similarity matrix and used the 2.5th and 97.5th percentiles of the sample distribution of estimated coefficients from 250 individual runs.

In the second part of the analysis, we applied generalized dissimilarity modelling (GDM) (Ferrier *et al.*, 2007) to investigate spatial and environmental drivers of turnover. GDM is specifically designed to analyse and predict large-scale patterns in beta diversity with respect to a set of explanatory variables. The model accounts for: (1) variation in the rate of turnover along individual variables and (2) the curvilinear relationship between compositional similarity and gradients of geographical or environmental separation (Ferrier *et al.*, 2007). This is achieved by producing a set of monotonically

increasing *I*-spline basis functions for each predictor and reformulating pairwise differences among sites as the differences along the *I*-spline basis functions. Coefficients for each basis function are calculated using maximum likelihood estimation in an inverse log-binomial GLM with compositional similarity as a response and the set of reformulated distances as predictors. The sum of fitted *I*-spline basis functions per predictor yields the final transformation function, representing the best-supported relationship between observed compositional similarity and pairwise distances along the considered predictor (Fitzpatrick *et al.*, 2013). The transformation functions provide two important pieces of information (Fig. 1). First, the total height of the curve serves as a proxy for the turnover associated with the respective environmental variable when all other variables are held constant. Second, the shape of the curve reflects the variation in the rate of turnover along the considered variable (Ferrier *et al.*, 2007).

Generalized dissimilarity models for each subset were fitted with the R-package *gdm* (Manion *et al.*, 2015), using a geographical distance matrix and the untransformed vectors of mean annual temperature, annual precipitation, temperature seasonality, precipitation seasonality, area and elevation as predictor variables of compositional similarity. We used the default setting of three *I*-spline basis functions per predictor. Significance testing of variables was realized by a combination of Monte Carlo sampling and stepwise backward elimination as implemented in the *gdm.varImp* function. We performed 250 permutations per step until only significant ($\alpha = 0.05$) variables remained in the model.

We used two different approaches to assess the importance of predictor variables which respectively reflect the *level importance* and *dispersion importance* (Achen, 1982; Grömping, 2006) with respect to compositional similarity. Dispersion importance, i.e. the amount of variance explained, was quantified by fitting separate GDMs using the full set of significant predictors (full model), only geographical distance (distance-only model) and only environmental variables (environment-only model). Based on the models' *deviance explained*, the metric of model fit in GDM, we partitioned the variation in compositional similarity into purely spatial, purely environmental, shared and unexplained effects (Borcard *et al.*, 1992; Legendre, 2008). For assessing level importance, i.e. the importance of a predictor for the response's mean, we followed Fitzpatrick *et al.* (2013) and used the height of significant transformation functions in the full model. To improve comparability between methods, heights were linearly rescaled so that their sum equals the proportion of deviance explained by the model.

Finally, we used GDM to derive predictions of compositional similarity across a global grid of 2986 equal-area grid cells (*c.* 50,000 km² per cell) on the basis of the distance-only, environment-only and full model for the mainland subset. Observed and predicted pairwise similarities were subjected to non-metric multidimensional scaling (NMDS) using the metaMDS function of the R-package *vegan* (Oksanen *et al.*, 2013). This yielded a quasi-optimal representation of pairwise similarities in a three-dimensional space. The

orientation of the NMDS objects was aligned perpendicular to the vectors of mean annual temperature and mean annual precipitation. The resulting vectors of *x*, *y* and *z* coordinates were individually rescaled to a range between 0 and 1 and projected into the red–green–blue colour space. This allowed us to visually assess the model performance and to create the first-ever global map of floristic similarity.

All analyses were carried out with the R statistical programming language v.3.2.3 (R Core Team, 2016).

RESULTS

Across all subsets, compositional similarity showed a pronounced decay with geographical distance, but the rate of decay (quantified as halving distance, $D_{S/2}$) differed strongly. The overall similarity of plant species assemblages declined by 50% every 1576 km (Fig. 2a). Island OGUs ($D_{S/2} = 1840$ km) showed a lower turnover rate than mainland OGUs ($D_{S/2} = 1216$ km). This pattern was consistent across taxonomic and functional subsets and was most pronounced for trees (Appendices S4 & S5). Also when inspecting the overall turnover rates for different island types (Fig. 2b), neither continental ($D_{S/2} = 1,384$ km) nor oceanic islands ($D_{S/2} = 1628$ km) exhibited a higher turnover rate than mainland OGUs. Moreover, we found very low turnover for atolls ($D_{S/2} = 5967$ km). Taxonomic and functional groups exhibited different distance decay patterns as well (Fig. 2c). The halving distance of angiosperms ($D_{S/2} = 1544$ km), with 95% of all species records the largest taxonomic subset, was very close to that of the full dataset (see Fig. 2c versus 2a). Gymnosperms ($D_{S/2} = 1476$ km) showed similarly high turnover to angiosperms, while pteridophytes ($D_{S/2} = 2156$ km) had the lowest turnover rate. Among functional groups (Fig. 2d), shrubs ($D_{S/2} = 826$ km) had a higher turnover rate than trees and herbs ($D_{S/2} = 1163$ km and 1523 km, respectively).

According to generalized dissimilarity modelling, geographical distance and environmental variables accounted for a combined 56–85% of compositional variation in the investigated subsets. The shapes of transformation functions in the fitted GDMs were broadly similar, indicating no fundamentally different responses along geographical and environmental gradients (Appendix S7). However, the relative importance of predictor variables differed strongly across subsets (Fig. 3). The variance-based approach generally tended to assign a higher importance to geographical distance than the transformation-based approach, such that the shared effects drew more strongly from the contribution of environmental variables. Contrary to our expectations, both methods concordantly showed a higher importance of geographical distance on the mainland, whereas environmental variables were considerably more important on islands. Looking at particular island types, we found the importance of environmental variables versus geographical distance to increase from continental islands to oceanic islands to atolls (Fig. 3). Moreover, atolls stood out due to strong effects of precipitation seasonality and the non-significance of all other

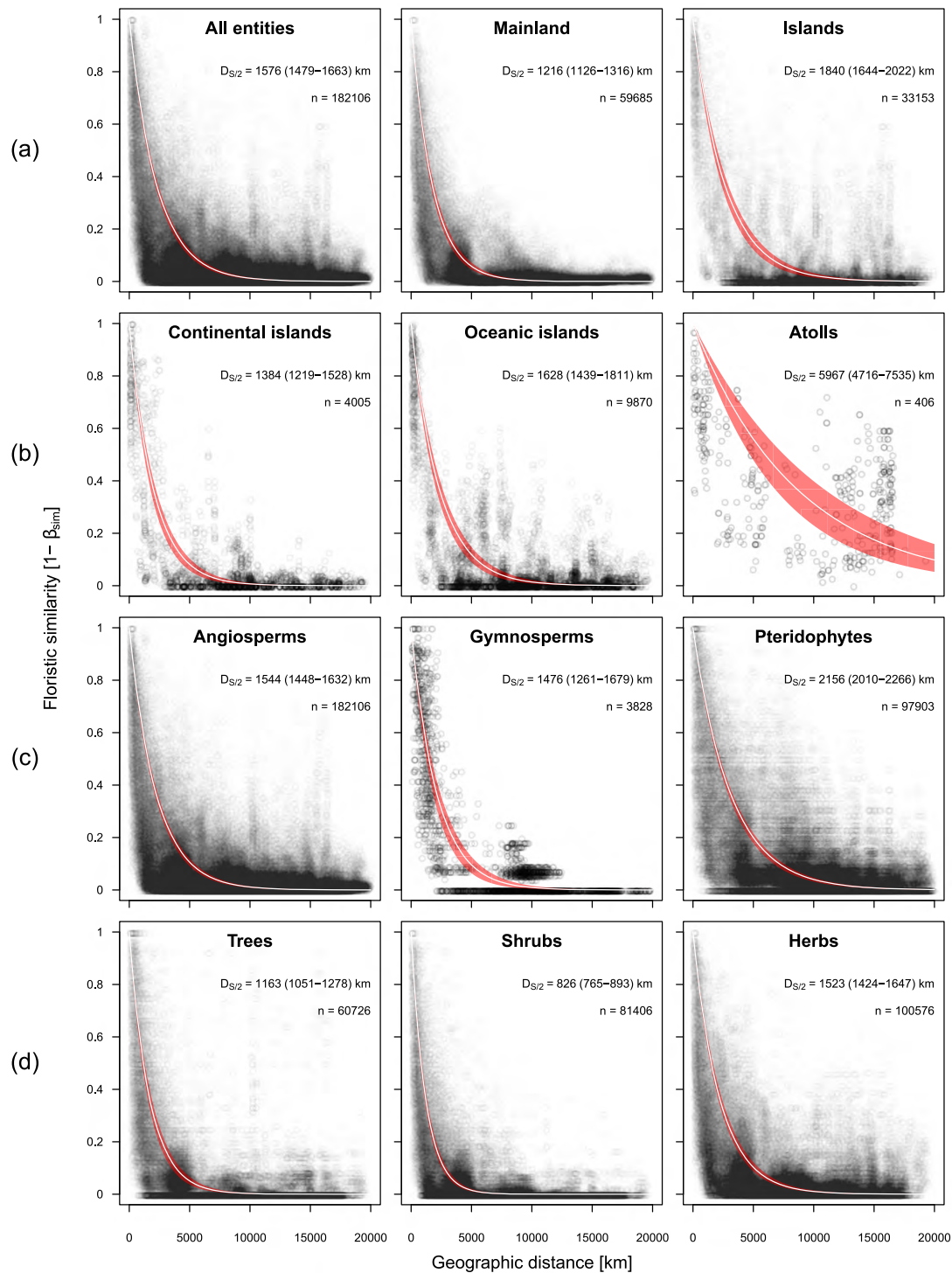


Figure 2 Distance decay of similarity for different subsets based on (a) geographical setting, (b) island type, (c) taxonomic group and (d) functional group. For each subset, $D_{50/2}$ denotes the distance after which similarity decreases by 50% (halving distance) and n denotes the number of unique pairwise combinations within the subset. Regression lines (white) were fitted using a log-binomial generalized linear model (GLM) with intercept of 1. Confidence intervals (red) were computed by subsampling the data 250 times, refitting the model and taking the 2.5th and 97.5th percentiles of the sampling distribution of coefficient estimates.

environmental variables. However, it must be acknowledged that atolls, owing to their specific ontogeny, span only small environmental gradients. For instance, being located in the tropics, they cover a confined temperature range.

Taxonomic and functional subsets were quite similar with regard to the relative importance of predictor variables (Fig. 3). Only turnover in gymnosperms exhibited a substantially larger sensitivity to geographical distance compared with

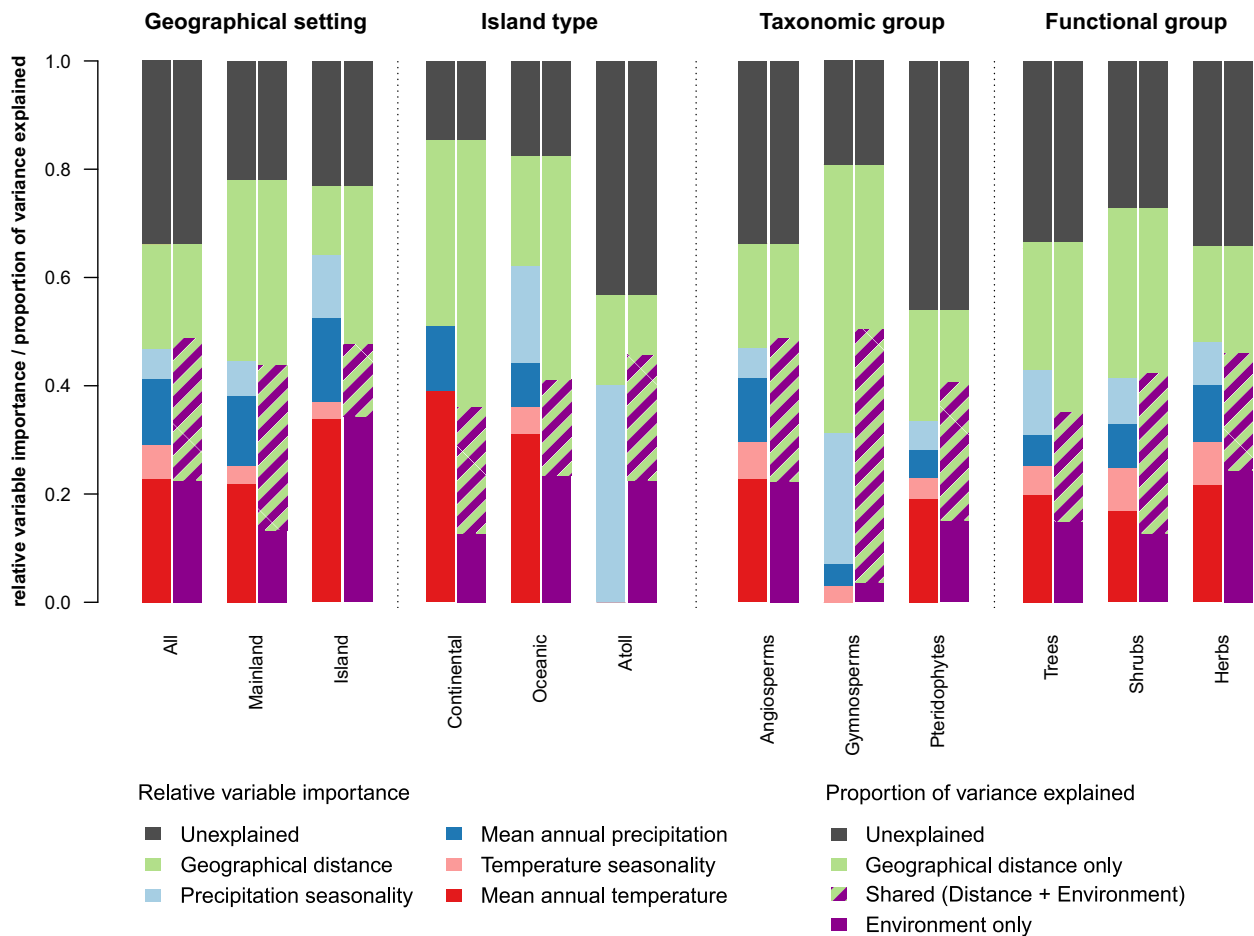


Figure 3 Turnover partitioning for taxonomic and functional groups, using generalized dissimilarity modelling (GDM). Results are shown for different subsets of the entire dataset based on geographical setting, island type, taxonomic, and functional group. For each subset, two alternative measures of variable importance are presented where the left-hand side is based on the height of GDM transformation functions and the right-hand side is based on variation partitioning.

other subsets. However, we obtained more heterogeneous results when we analysed turnover of individual groups for island and mainland OGUs separately (Appendix S6). Here, turnover again showed a consistent shift towards stronger environmental control and lower importance of geographical distance on islands compared with the mainland. Tree turnover exhibited the strongest contrast, while the differences were least pronounced for pteridophytes. The shift in variable importance was generally stronger in the transformation-based than the variance-based approach. For shrubs, the variance-based approach even indicated a higher importance of geographical distance on islands. No GDM could be fitted for gymnosperms on islands because only seven OGUs met our inclusion criteria.

Our predictions of global compositional similarity (Fig. 4) illustrate how turnover results from a combination of spatial and environmental determinants. Notably, the predictions of the environment-only model closely resemble biomes and reflect the expected compositional similarity in the absence of dispersal limitation and biogeographical history. The distance-only model, in contrast, depicts the expected

similarity in the absence of environmental limitations. A visual comparison of observed versus predicted similarities (Fig. 4) confirms that GDM is able to accurately model large-scale turnover patterns in continuous environments, albeit predictions became less accurate in regions with a unique biogeographical history (e.g. Australia and South Africa).

DISCUSSION

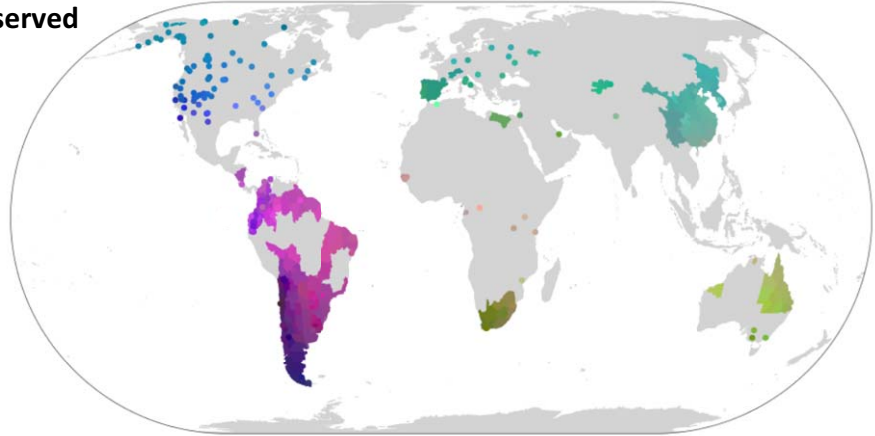
In general, global turnover in vascular plants was remarkably well explained by a combination of geographical distance and a small set of climatic predictors. However, our analyses revealed considerable differences among geographical settings as well as functional and taxonomic groups in the total amount of turnover and the relative importance of its spatial and environmental drivers.

Turnover as result of filtering processes

Unexpectedly, turnover among islands was lower than among mainland OGUs and generally more associated with environmental variables than with geographical distance (Figs 2 & 3).

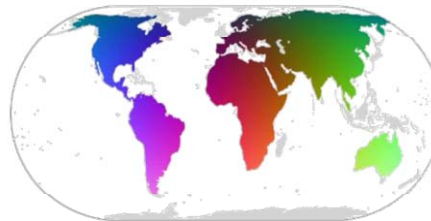
Compositional similarity

Observed

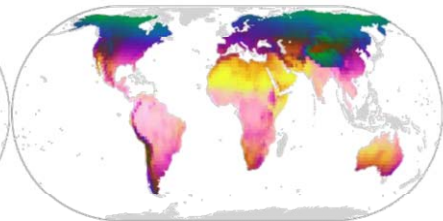


Modelled

Distance



Environment



Distance and environment

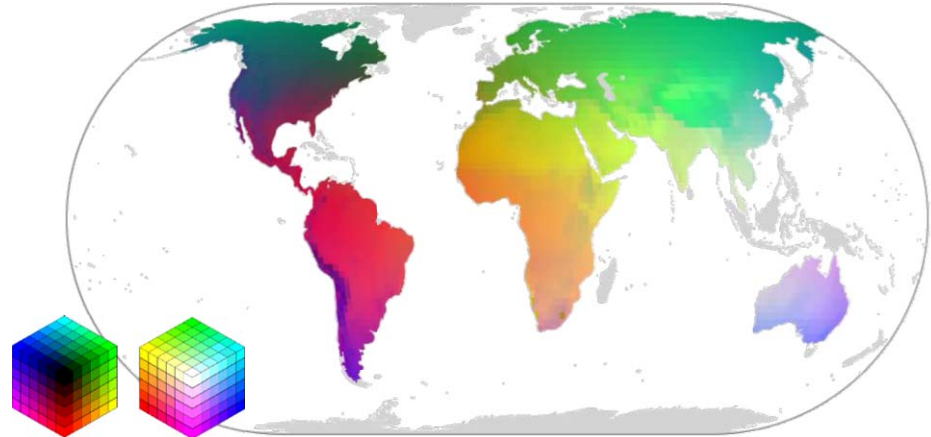


Figure 4 Predicted compositional similarity of vascular plants for 2986 equal-area grid cells of c. 50,000 km² size. Predictions are derived from a generalized dissimilarity model fitted with geographical, environmental and floristic information for 346 mainland operational geographical units. Predicted similarities were subjected to a three-dimensional non-metric multidimensional scaling, standardized, and projected into RGB-colour space. Similar colours indicate grid cells with similar predicted species composition. Center left- and right-hand panels show model predictions for geographical distance and environmental conditions only. Lower panel depicts the predicted similarities based on the full model. Projection: Eckert IV.

This finding seems to contradict the general notion of islands as isolated microcosms, featuring unique biota (Gillespie, 2001). However, these results become comprehensible when shifting the perspective from iconic, isolated archipelagos such as Hawaii towards a more general view on islands. Islands are surrounded by inhospitable open sea which presents a strong dispersal filter to the immigrating species (Carlquist, 1965; Whittaker & Fernández-Palacios, 2007). On the other hand, local conditions on islands impose an environmental filter upon the climatic tolerances, habitat preferences or reproductive strategies of arriving species (Carlquist, 1965; Weigelt *et al.*, 2015). A lower turnover rate among islands can thus be explained by these filtering processes reducing the set of potential colonizers and thereby homogenizing the composition of realized species assemblages.

Additionally, the particularly strong dispersal filter associated with islands may be passed only by dispersive – and therefore rather distance-insensitive – species, which explains the reduced importance of geographical distance for turnover on islands (Fig. 3, Appendix S6).

Atolls make a strong case for the interpretation of turnover being the result of filtering processes. The conditions on atolls impose both very strong dispersal and environmental filters that may be passed by only a few species that are both highly dispersive and adapted to tropical temperatures, coastal conditions (e.g. high salinity, high levels of disturbance) and small population sizes. Consequently, we found very low turnover among atolls and a low sensitivity to geographical distance (Figs 2 & 3), confirming previous, more descriptive, analyses (Stoddard, 1992). Systems that exhibit

relaxed filtering, such as oceanic islands (reduced environmental filtering) or continental islands (reduced dispersal and environmental filtering), however, sample from a larger pool of potential colonizers and are thus characterized by higher turnover rates. This rationale may also help to understand other prominent biogeographical patterns, including latitudinal or elevational gradients in beta diversity (Qian & Ricklefs, 2007; Tello *et al.*, 2015). For example, it suggests that the size of the species pool (gamma diversity) is an inherent property of the geographical or environmental setting and that correcting for variations in pool size (Kraft *et al.*, 2011) might lead to incorrect conclusions regarding the role of assembly processes.

The above considerations do not address the main reason why island biota are regarded as unique, namely endemism. Islands are hotspots of *in situ* diversification (Kier *et al.*, 2009) and endemic species are potentially a strong driver of turnover among islands. The impact of endemism on turnover is proportional to the fraction of endemic species in a flora. While this fraction may be quite high for large, isolated islands, the majority of islands represent smaller and less isolated geographical entities (Weigelt *et al.*, 2013). From the 115 island OGUs in our dataset with available information on endemism status, 90 had fewer than 10% endemics. Thus, the native flora of most islands consists predominantly of rather widespread non-endemic species and is a product of strong dispersal and environmental filtering, resulting in reduced turnover. Supporting this, the most frequently shared species among islands in our dataset were invariably pantropical coastal and littoral plants such as *Scaevola taccada*, *Cassytha filiformis*, *Fimbristylis cymosa* or *Ipomoea pes-caprae*. While studies on other groups of organisms report different results (e.g. Stuart *et al.*, 2012), the overall effect of endemism on the compositional structure of plant assemblages on islands may be smaller than expected.

The role of species attributes for turnover

As illustrated by the small set of widespread littoral plants on islands, the ability to pass ecological filters depends on species attributes like dispersal ability or environmental tolerance. This is reflected by group-specific turnover patterns. According to our analyses, turnover rates were lowest for pteridophytes, intermediate for angiosperms, gymnosperms and herbs, high for trees and very high for shrubs (Fig. 2). Similar results at smaller scales were reported by Tuomisto *et al.* (2003) and Qian (2009) for angiosperms versus pteridophytes, and by López-Martínez *et al.* (2013) for shrubs versus trees. Our findings align well with the average propagule size, and thus approximate dispersal ability, of the investigated groups (Levin, 1974; Westoby *et al.*, 1996; Moles, 2005) and further confirm a negative relationship between dispersal ability and turnover (Nekola & White, 1999; Tuomisto *et al.*, 2003; Qian, 2009).

The relative importance of geographical distance and environmental variables for turnover was rather similar across

functional and taxonomic groups (Fig. 3). When contrasting group responses in mainland and island systems, however, we found a consistently elevated importance of environmental variables and reduced importance of geographical distance on islands (Appendix S6). Notably, the shift in variable importance was strongest for groups with high sensitivity to geographical distance on the mainland, suggesting that these are more strongly affected by the increased level of dispersal filtering on islands. Consequentially, only a small, highly dispersive fraction of these groups is represented on islands, leading to the inversion of variable importance and the low relative importance of geographical distance. Gymnosperms on islands mark an extreme case of this effect: here, the strength of dispersal filtering apparently surpasses the group's dispersal abilities to such an extent that it is almost entirely absent from this geographical setting (see Appendices S4 & S6).

While our results demonstrate a clear relationship between turnover and group-specific dispersal abilities, the linkage between turnover and environmental group characteristics is less evident. However, assumptions regarding group differences in dispersal ability can be reasonably justified on the basis of average propagule sizes and characteristic reproductive strategies. In contrast, a similar evaluation of the considered groups with respect to environmental tolerances is more difficult. A rigorous test of the relationships between species characteristics and environmental filtering would require a detailed *a priori* definition of groups based on features that are causally linked to niche breadth and independent of dispersal ability. Given the recent progress in estimating niche dimensions (Kearney *et al.*, 2010; Blonder *et al.*, 2014; Díaz *et al.*, 2016) and the increasing availability of functional trait data (Kattge *et al.*, 2014), we are confident that such analyses will soon be within reach.

The origin of beta diversity

Although estimates of variable importance were plausible in the context of specific geographical settings and species groups, it is difficult to draw a general conclusion regarding the balance of spatial and environmental drivers of vascular plant turnover. The two measures of variable importance produced slightly different results, with the variance-based approach putting more weight on geographical distance than the transformation-based approach. Considering the way these methods work, this difference highlights some important properties of large-scale beta-diversity patterns. Most of the systematic change in compositional similarity occurred within the first 3000–5000 km, whereas pairwise similarity was generally low thereafter (Fig. 2). Hence, for the 75–85% of site pairs that lie beyond that threshold, almost complete turnover is predicted very accurately by geographical distance alone. This is reflected by the high importance of geographical distance in the variance-based approach. In contrast, the transformation-based approach is more robust against the high number of low values of compositional similarity at large geographical distances: If a further change in a

predictor does not affect compositional similarity, the transformation function flattens out and the variable importance remains constant. This, however, does not allow us to address multicollinearity among predictors by estimating shared effects. In summary, the variance-based approach is best understood as reflecting the *overall* prediction accuracy of a variable, whereas the transformation-based approach indicates the importance of a variable for *systematic* changes in compositional similarity.

Relating this to our results, both methods clearly show that environmental and spatial factors act jointly in causing turnover in vascular plants. For most subsets, the systematic change in composition is slightly more controlled by environmental conditions than by geographical distance. With increasing geographical distance, however, compositional similarity generally approaches very low values and environmental variables become increasingly expendable for predicting turnover. Topographical site properties such as elevation and area did not have important effects at the studied spatial grain and extent. The consideration of scaling effects is crucial when approaching the question of whether niche-based or neutral processes drive global turnover. Chase (2014) provides compelling arguments why the importance of neutral processes should diminish with increasing spatial scale. At such scales, unique effects of geographical distance are more likely to be the product of evolutionary history than of neutral immigration–extinction dynamics. Moreover, it is important to note that dispersal, although partly stochastic, is not necessarily a neutral process: species clearly differ in their dispersal ability which (1) violates the assumption of species equivalence in neutral models and (2) adds a deterministic component to the process of dispersal (Lowe & McPeck, 2014). Equating distance-related effects on species composition with the importance of neutral processes would therefore disregard the signal of non-random species filtering. According to our results, global turnover in vascular plants is structured by a combination of niche-based processes related to environmental factors and predominantly non-neutral dispersal- and speciation-related processes related to geographical distance.

Methodological strengths and limitations

The nature of large-scale beta-diversity data presents some statistical challenges due to the high number of low and zero values. In contrast to the distance decay models, generalized dissimilarity modelling is relatively robust under these circumstances and proved to be a powerful tool for analysing turnover, with our predictions of mainland compositional similarity (Fig. 4) showcasing only one application. A mechanistic understanding of beta diversity is increasingly recognized as a key requirement for the effective protection of global biodiversity (Socolar *et al.*, 2016). Complex statistical models such as GDM are a promising way to further develop this understanding and to derive accurate predictions of ecosystem responses under future conditions (Mokany *et al.*, 2016). A next promising step towards this objective is to integrate phylogenetic information into the modelling

framework (Graham & Fine, 2008; Rosauer *et al.*, 2014). This may reduce the problem of zero inflation, increase the informational resolution of the data, and allow us to disentangle the role of evolutionary history and dispersal limitation in the spatial signal of compositional similarity.

CONCLUSION

Our results demonstrate a complex interplay of geographical and environmental factors as well as species characteristics in determining the magnitude and structure of turnover. We found strong evidence that: (1) the geographical setting affects turnover via dispersal and environmental filtering and (2) the ability to pass these filters varies among taxonomic and functional groups and is largely congruent with expectations based on group-specific attributes, particularly with dispersal ability. However, while the relationship between species attributes and turnover has received a fair amount of attention during the last decades, our findings suggest that the geographical context may play an equal, if not more important, role in shaping patterns of turnover. Addressing the specific ecological filters that are associated with different geographical settings may help to better understand large-scale patterns in beta diversity. For this purpose, the application of powerful statistical models such as GDM in combination with phylogenetic data offers great potential.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Summary of the 258 island and 346 mainland operational geographical units (OGUs) analyzed in this study. In all panels, island OGUs are depicted blue and mainland OGUs are depicted red. (a) Geographical distribution, Projection: Eckert IV, (b) Histogram of area per OGU, (c) Histogram of species number per OGU and (d) Major climatic characteristics of OGUs plotted in Whittaker biome space (Whittaker, R.H. (1970). *Communities and ecosystems*. Macmillan, New York).

Appendix S2 Graph structure used to derive plant growth form from other available functional traits. Greyed out fields indicate that there is no meaningful derivation for the respective trait. Dotted lines indicate derivations that were not used in this study.

Appendix S3 Pairwise correlation of predictor variables used in GDM. Lower left triangle: Scatterplot for pairs of variables and LOESS-fit (red line), Diagonal: Histogram and variable abbreviations, Upper right triangle: Pearson correlation coefficients between pairs of variables. The highest observed variance inflation factor (not shown) was 3.25 for mean annual temperature (T_mean), suggesting no problematic amounts of multicollinearity among predictors.

Appendix S4 Distance decay for taxonomic and functional groups (island vs. mainland comparison). $D_{S/2}$ denotes the distance after which similarity decreases by 50% (halving distance) and n denotes the number of unique pairwise combinations within each subset. Model coefficients (dots) were obtained using a log-binomial generalized linear model (GLM) with an intercept of 1. Confidence intervals (whiskers) were computed by subsampling the data 250 times, refitting the model and taking the 2.5 and 97.5 percentiles of the sampling distribution of coefficient estimates. No significant model was obtained for subset 'gymnosperms × island'.

Appendix S5 Distance decay model summaries. Halving distance ($D_{S/2}$) denotes the distance after which similarity decreases by 50 % and n denotes the number of unique pairwise combinations within each subset. Model coefficients ('beta_hat') were obtained using a log-binomial generalized

linear model (GLM) with an intercept of 1. Confidence intervals ('beta_CI_min' and 'beta_CI_max') were computed by subsampling the data 1000 times, refitting the model and taking the 2.5 and 97.5 percentiles of the sampling distribution of coefficient estimates. Significance levels: ***- $p < 0.001$; n.s. – not significant.

Appendix S6 Turnover partitioning for taxonomic and functional groups (mainland vs. island comparison) using generalized dissimilarity modelling. Results are shown for different subsets of the entire dataset based on geographical setting, island type, taxonomic, and functional group. For each subset, two alternative measures of variable importance are presented where the left-hand side is based on the height of GDM transformation functions and the right-hand side is based on variation partitioning. No GDM could be fitted for gymnosperms on islands.

Appendix S7 GDM transformation functions for subsets based on (a) geographical setting, (b) island type, (c) taxonomic and (d) functional group. Units of measurement were adopted unchanged from WorldClim (Hijmans *et al.*, 2005).

BIOSKETCHES

Christian König is a PhD candidate at the University of Göttingen and is interested in the mechanisms that underlie large-scale biogeographical patterns. In his research he uses vascular plants as model organisms to investigate different aspects of taxonomic, functional and phylogenetic diversity.

Patrick Weigelt is fascinated by the global distribution patterns of plants and the past and present drivers and underlying mechanisms that shape them. He uses island floras as model systems to investigate the roles of dispersal, speciation and extinction for the composition of plant assemblages.

Holger Kreft is interested in biogeographical and ecological patterns from local to global scales, particularly gradients of species richness and endemism. His research includes analyses of plant and vertebrate diversity, and island and conservation biogeography.

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APPENDIX 1: DATA SOURCES

CHECKLIST RESOURCES

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