Disharmony of the world's island floras

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Abstract

Disharmony is a key concept in island biology that describes the biased representation of higher taxa on islands compared to their mainland source regions. Although differential colonization success of taxa is predicted by selective dispersal, environmental and biotic filtering, the empirical evidence for disharmony remains largely anecdotal. Here, we develop a novel method for delineating island source regions and present the first global quantitative assessment of island disharmony. We analyzed the overall compositional bias of 320 island floras and examined the over- or under-representation on islands for 450 plant families. We found that the compositional bias of island floras is strongly predicted by geographical and climatic island characteristics (isolation, area, geologic origin, temperature, precipitation), whereas the representation of individual families is only weakly related to family-specific characteristics (family size, family age, taxonomic group, functional traits), indicating that the taxonomic scope of the disharmony concept has historically limited its wider applicability. Our results provide a strong foundation for integrating disharmony with quantitative functional and phylogenetic approaches in order to gain a deeper understanding of assembly processes on islands.

Introduction

Islands are renowned for their unique biotas, often characterized by high levels of endemism (Kier *et al.* 2009), species radiations (Böhle *et al.* 1996; Givnish *et al.* 2009), relictual taxa (Vargas 2007) or peculiar shifts in species' life history and morphology (Carlquist 1965). These features can be attributed to the isolated nature of islands (Weigelt & Kreft 2013), which strongly affects the fundamental processes controlling species diversity: immigration, speciation, and extinction. Thus, research on island systems has stimulated many seminal contributions to evolutionary (Darwin 1859; Wallace 1881) and ecological theory (MacArthur & Wilson 1963, 1967; Hubbell 2001; Whittaker *et al.* 2008). The island biogeographical studies by Carlquist (1965, 1967, 1974) are undoubtedly among these seminal contributions, providing substantial insights into processes such as long-distance dispersal or adaptive radiation, and inspiring island research to this date (Traveset *et al.* 2015). In contrast to the strictly analytical approach of MacArthur & Wilson's equilibrium theory of island biogeography (1963, 1967), Carlquist's work offers mostly a natural history perspective. While this perspective does not allow for quantitative predictions of e.g. species richness, it is a powerful framework for understanding qualitative features of island biota such as taxonomic composition or morphological adaptations (Midway & Hodge 2012). One such feature is the striking taxonomic "imbalance" of many island biotas– a phenomenon known as disharmony (Carlquist 1974, 1965).

Island disharmony refers to the biased representation of higher taxa (e.g. families) in island biotas compared to their mainland source regions (Whittaker & Fernández-Palacios 2007). It is the result of selective assembly mechanisms – dispersal filtering, environmental filtering and biotic filtering (Carlquist 1974; Keddy 1992; Weiher *et al.* 2011; Kraft *et al.* 2015) – acting with particular rigor in island systems, thus permitting only a subset of the mainland flora to successfully colonize islands. The interplay between geographical setting and taxon-specific colonization success highlights two distinct aspects of island disharmony. On the one hand, the overall compositional bias of island floras relative to their mainland source regions (compositional disharmony) should reflect the impact of ecological filters during their assembly, and thus show predictable variation with island-specific characteristics such as isolation, area, climatic conditions, or geological origin. On the other hand, the selectivity of these filters should result in a predictable over- or under-representation of individual taxa on islands (representational disharmony) that is associated with taxon-specific attributes related to e.g. dispersal ability or environmental tolerances. Indeed, numerous studies demonstrate that community composition of island floras is strongly dependent on geographical setting (Whittaker *et al.* 2008; König *et al.* 2017) and taxon-specific attributes (Burns 2005; Olesen *et al.* 2010).

While the theoretical underpinnings of island disharmony are well established, the concept itself has been applied rather inconsistently and lacks a quantitative basis. In particular, the specification of

mainland source regions is not trivial and often very coarse (Bernardello *et al.* 2006) and the taxonomic bias of island floras is usually illustrated by means of anecdotal evidence rather than objective quantitative measures (Francisco-Ortega *et al.* 2010). In addition, there has been little work on whether the over- or under-representation of certain plant taxa on islands is globally consistent or not (but see e.g. Kreft *et al.* 2010 on the over-representation of ferns in island floras), and whether representational deviations are linked to taxon-specific attributes that supposedly affect colonization success (but see e.g. Grossenbacher *et al.* 2017). Consequently, the empirical evidence for island disharmony remains fragmentary.

Here, we provide the first quantitative analysis of island disharmony for vascular plants using an unprecedented dataset of 320 island and 611 mainland floras including a total of 225,053 species. First, we present a novel method for estimating island-specific source regions and develop two mathematical indices that quantify compositional and representational disharmony. This enabled us to examine the phenomenon of disharmony from an island- and a taxon-centred perspective, and thus to disentangle its island-specific and taxon-specific drivers. Accordingly, we analyze compositional disharmony as a function of island isolation, area, geological origin, and climatic conditions, and representational disharmony as a function of families' species richness, age, range size and predominant functional characteristics related to colonization success. In particular, we are interested in the importance of dispersal, environmental and biotic filtering in creating disharmonic island floras. If dispersal filtering is the dominant cause of disharmony (Carlquist 1967, 1974), we would expect strong positive effects of isolation on compositional disharmony as well as a consistently positive effect of dispersal-related traits on representational disharmony. Alternatively, if environmental or biotic filtering processes play an important role (Carvajal-Endara *et al.* 2017; Grossenbacher *et al.* 2017), we expect to find a strong response of compositional and representational disharmony to island climatic variables and pollination or competition-related traits, respectively.

Methods

We examined the phenomenon of island disharmony from both an island- and a taxon-centred perspective (Figure 1). First, we assessed compositional disharmony, i.e. the phenomenon of island floras being taxonomically biased compared to their mainland source regions. Second, we investigated representational disharmony, i.e. the role of individual taxa in creating compositional disharmony by assessing their global representation on islands compared to the mainland. In both cases, we chose families as the focal taxonomic level. Given that disharmony is explicitly about the representation of higher taxonomic groups on islands, families provide a reasonable compromise between ecological uniformity and taxonomic aggregation. In contrast, higher taxonomic levels such as orders encompass too many species that are too heterogeneous in their attributes to be ecologically meaningful study

units, whereas lower levels such as genera are too numerous to be harmonically represented in any island flora.

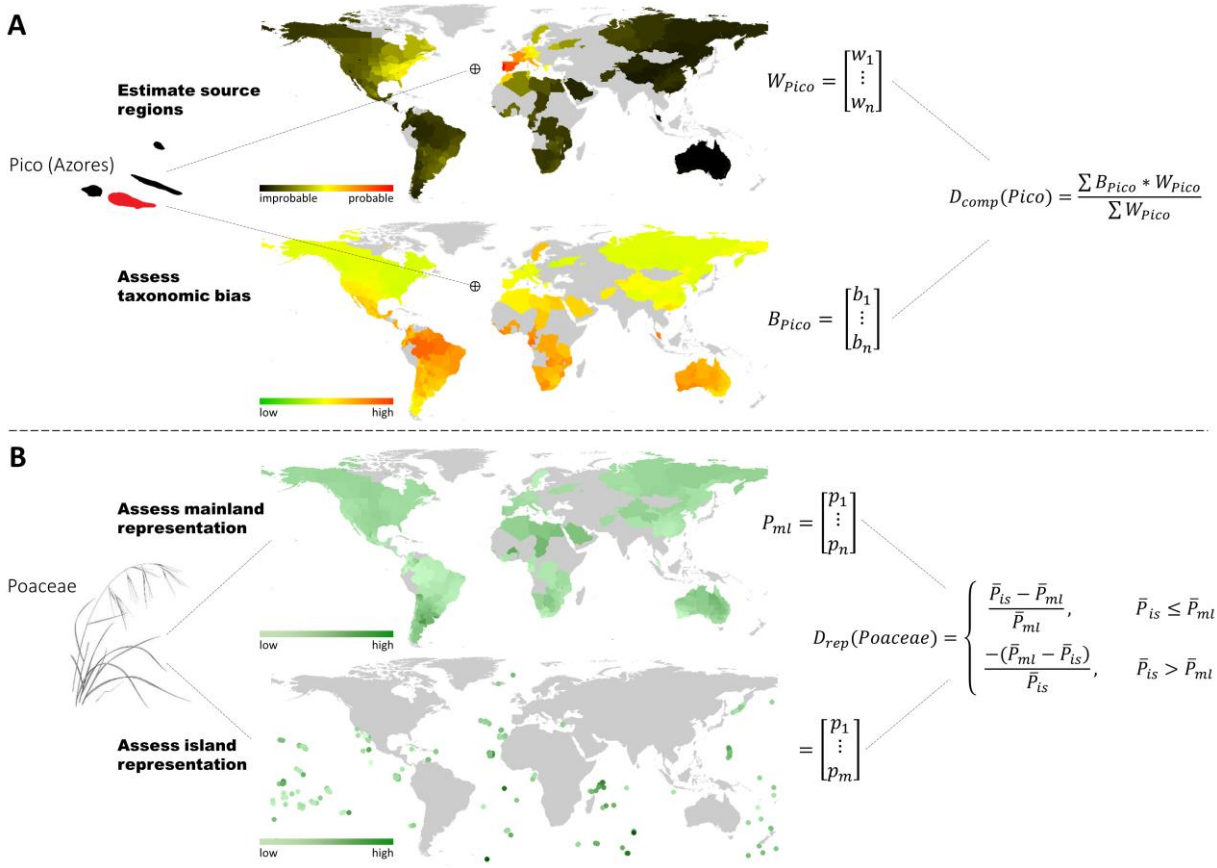

Figure 1: Schematic representation of the quantification of compositional and representational disharmony. (A) Calculation of compositional disharmony by the example of Pico Island (Azores). Source regions were estimated based on predictions of species turnover between the focal island and all mainland units (W, upper plot). The taxonomic bias between the focal island and all mainland units was quantified using Bray-Curtis dissimilarity on relative proportions of plant families (B, lower plot). The compositional disharmony of the focal island (D_{comp}) was then calculated as the mean taxonomic bias relative to all mainland regions, weighted by their respective source region weight. (B) Estimation of representational disharmony by the example of Poaceae. Representational disharmony was quantified based on the mean proportion of the focal taxon in mainland floras ($\bar{P}_{ml}$) and island floras ($\bar{P}_{is}$). The corresponding index (D_{rep}) transforms the ratio between these two components to a range between -1 (family occurs on the mainland only) and 1 (family occurs on islands only).

Data collection

All ecological and environmental data were obtained from GIFT, the Global Inventory of Floras and Traits database (Weigelt *et al.* 2018), a comprehensive resource for macroecological analyses of global plant diversity. The primary data type in GIFT are regional plant checklists that are integrated with additional information at the level of taxa (e.g. functional traits, taxonomic placement, phylogenetic relationships, or floristic status) and geographical units (e.g. climatic and environmental conditions, socioeconomic factors or physical geographic properties).

From GIFT, we extracted all checklists that indicate the nativeness status of the species listed and excluded non-native species from all further analyses. Checklist completeness was evaluated based on the reference type (e.g. multi-volume Floras being more reliable than rapid assessments), the

general text included in the reference (e.g. statements regarding sampling effort, timeframe, or use of additional data sources), and general properties of the species list (e.g. plausible number of species for the given area and biome, species-to-genus ratio, presence of regionally important taxa). Checklists with considerable deficits in either of these categories were excluded. We then combined checklists referring to the same geographical unit and removed all geographical units that were not covered by either a complete checklist of vascular plants or by several checklists that add up to a complete checklist of vascular plants (e.g. separate lists for pteridophytes and seed plants). The resulting dataset contained native vascular plant checklists for 611 mainland and 320 islands units (see SI data references).

Compositional disharmony

Quantification

The quantification of compositional disharmony requires estimates of island-specific source regions and an objective measure of taxonomic bias (Figure 1A). We based our method for estimating source regions on the fact that geographic distance and environmental gradients produce distinct and predictable patterns in species turnover (Fitzpatrick *et al.* 2013; König *et al.* 2017). Species turnover is a richness-insensitive measure of compositional similarity that quantifies the proportion of shared species between assemblages (Baselga 2010). This makes turnover a crucial concept for constructing biogeographical species pools and delineating source regions (Carstensen *et al.* 2013).

We used generalized dissimilarity modelling (Ferrier *et al.* 2007) to model species turnover (β_{sim}, Koleff *et al.* 2003) among geographical units as a function of pairwise geographic distance and differences in mean annual temperature, mean annual precipitation, temperature seasonality and precipitation seasonality. These covariates are strong predictors of large-scale species turnover (König *et al.* 2017). The model was fitted using mainland data only (deviance explained = 80.5%), because island floras exhibit strong imprints of ecological filtering, which would mask the very effects we aim to quantify in this study. We derived model predictions of species turnover between each island and a global equal-area, equidistant hexagon grid (~ 23,300 km² per cell) covering all continents and important island source regions. The predictions were then aggregated to the level of the GIFT mainland units by calculating the area-weighted mean of grid values per unit (Figure 1A). The resulting $m \times n$ matrix, $\mathbf{W}$, contained the expected proportion of shared species (1- β_{sim}) between all m islands and all n mainland units from a "mainland perspective", i.e. assuming that island floras assemble under the same conditions as floras on the mainland. The matrix W can thus be interpreted as reflecting the importance of a given mainland unit as a source region for a given island, while excluding the effects of modified filtering during island colonization. We set $\mathrm{W} = 0$ for mainland units with very low values,

i.e. highly improbable source region for a given island, to ensure a balanced estimation of compositional disharmony (see SI Text 1 for details). To validate our method, we compared the results with empirical source region reconstructions based on floristic and phylogenetic relationships to the mainland.

To assess the actual taxonomic bias of an island flora, we converted the species checklists to relative family proportions in order to account for species richness differences. We then calculated the Bray-Curtis dissimilarity for all pairwise island-mainland combinations, yielding an $m \times n$ matrix, $\mathbf{B}$. The Bray-Curtis index is the abundance-based version of the Sørensen index that relates the summed differences between two variables to their overall sum. Although usually applied to count data, the index also works with relative proportions (Greenacre & Primicerio 2013), making it an appropriate measure of taxonomic bias.

Finally, we calculated the compositional disharmony of each island, $\mathbf{D}_{\mathrm{comp}}$, as the mean taxonomic bias of a given island i relative to all mainland units ($\mathrm{B_i}$), weighted by their respective importance as a source region for the specific island ($\mathrm{W_i}$). $\mathrm{D_{comp}}$ ranges between 0 and 1, with higher values indicating more disharmonic floras (Figure 1).

Analysis

For each island, we calculated area (AREA; km²) and extracted averaged values for mean annual temperature (MAT; °C), mean annual precipitation (MAP; mm/a), temperature seasonality (TVAR; °C), and precipitation seasonality (PVAR; mm/a) from CHELSA climate layers (Karger *et al.* 2017). We additionally calculated the minimum distance to the nearest mainland (DIST), assessed the geological origin based on pertinent literature (GEO, distinguishing between shelf, continental fragment, volcanic, tectonic uplift and atoll, see König *et al.* 2017 for definitions), and respective island group (ARCH) for each island.

We $\log_{10}$-transformed AREA, DIST, MAP, TVAR and PVAR because of strongly skewed distributions. For MAT, no adequate transformation was found. We then scaled all continuous predictor variables to $\mu = 0$ and $\sigma = 1$ in order to standardize model coefficients. Although our response variable ($\mathrm{D_{comp}}$) is, in principle, a proportional value ranging from 0 to 1, it was effectively bound between 0.19 and 0.87, and approximately normally distributed within that interval. We therefore performed the analysis of compositional disharmony using standard linear mixed effects models. Following Bunnefeld & Phillimore (2012), we specified archipelago (ARCH) as random effect. Moreover, we included interactions between DIST and GEO, and AREA and GEO in order to reflect potentially varying effects of island isolation and area on compositional disharmony, depending on whether an island has once been connected to the mainland or not. Based on the full model ($D_{comp} \sim DIST{:}GEO +$

$AREA: GEO + MAT + MAP + TVAR + PVAR + GEO + (1|ARCH)$), we (1) fitted models for all possible combinations of predictor variables, (2) selected those models with the most empirical support (ΔAIC < 2), and (3) performed model averaging on this set of models (Barton 2016; Grueber *et al.* 2011). Unless stated otherwise, all reported effects are based on the averaged model results.

Representational disharmony

Quantification

For the quantification of representational disharmony, we developed a second index (D_{rep}) that is based on the mean proportional representation of the focal family across all mainland units ($\bar{P}_{ml}$) and all oceanic islands ($\bar{P}_{is}$, see Figure 1B). We focussed on oceanic islands (volcanic islands, tectonic islands and atolls) because their floras reflect the effects of dispersal, environmental and biotic filtering most clearly (Whittaker & Fernández-Palacios 2007) and thus allow for the most rigorous assessment of taxon-specific drivers of disharmony. The index is symmetric and obtains values in the interval $(-1, 1)$, with the sign indicating whether the focal family is proportionally more abundant on islands or on the mainland (SI Figure 1). For example, a family with $D_{rep} = 0.5$ has, on average, a two times higher proportion on islands as compared to the mainland, whereas a family with $D_{rep} = -0.9$ has a 10-times higher proportion on the mainland. The special cases of $D_{rep} = -1$, $D_{rep} = 0$ and $D_{rep} = 1$ indicate a family's restriction to the mainland, equal proportional representation on islands and the mainland, and restriction to islands, respectively.

Analysis

We obtained the total number of species in each family (SPEC) from The Plant List (The Plant List 2013) and supplemented it with values from Christenhusz & Byng 2016 where The Plant List did not resolve the respective family. The assignment of taxonomic supergroups (GROUP, distinguishing between angiosperms, gymnosperms and pteridophytes), family age estimates (AGE) and all further phylogenetic analyses were based on a recent megaphylogeny of vascular plants (Qian & Jin 2016). For seed plants only, we selected six functional traits reflecting dispersal ability (dispersal syndrome, fruit type, seed mass), life history (growth form) and reproductive characteristics (pollination syndrome, self-compatibility). For each trait, we aggregated all species-level information available in GIFT (see SI data references) to the family-level: for categorical traits, we assigned a value to a family when the majority (> 66 %) of the species level values in GIFT were identical, i.e. a predominant trait syndrome was evident for the respective family; for numerical traits, we calculated the median across all species in the respective family with information on the respective trait.

We used multiple linear regression to analyze representational disharmony (D_{rep}) as a function of GROUP, AGE and SPEC. We had to omit all functional trait variables because missing data points would

have drastically reduced the statistical power of the model. Instead, we analyzed the impact of traits on D_{rep} individually, using single-predictor linear models (for continuous traits) and one-way ANOVAs (for categorical traits). For significant categorical variables, we performed a Tukey HSD post-hoc test to identify systematic variation among variable levels.

To test for phylogenetic signal in D_{rep}, i.e. whether closely related taxa tend to be similarly over- or under-represented on islands, we calculated Abouheif's C_{mean} using the *phylosignal* R-package (Keck 2015). The C_{mean} index is a measure of phylogenetic autocorrelation that quantifies the squared differences between values (in this case D_{rep}) of neighboring tips in a phylogeny (Münkemüller *et al.* 2012).

All analyzes were performed in the R statistical programming language, version 3.4.4 (R Core Team 2017).

Results

Source region estimation

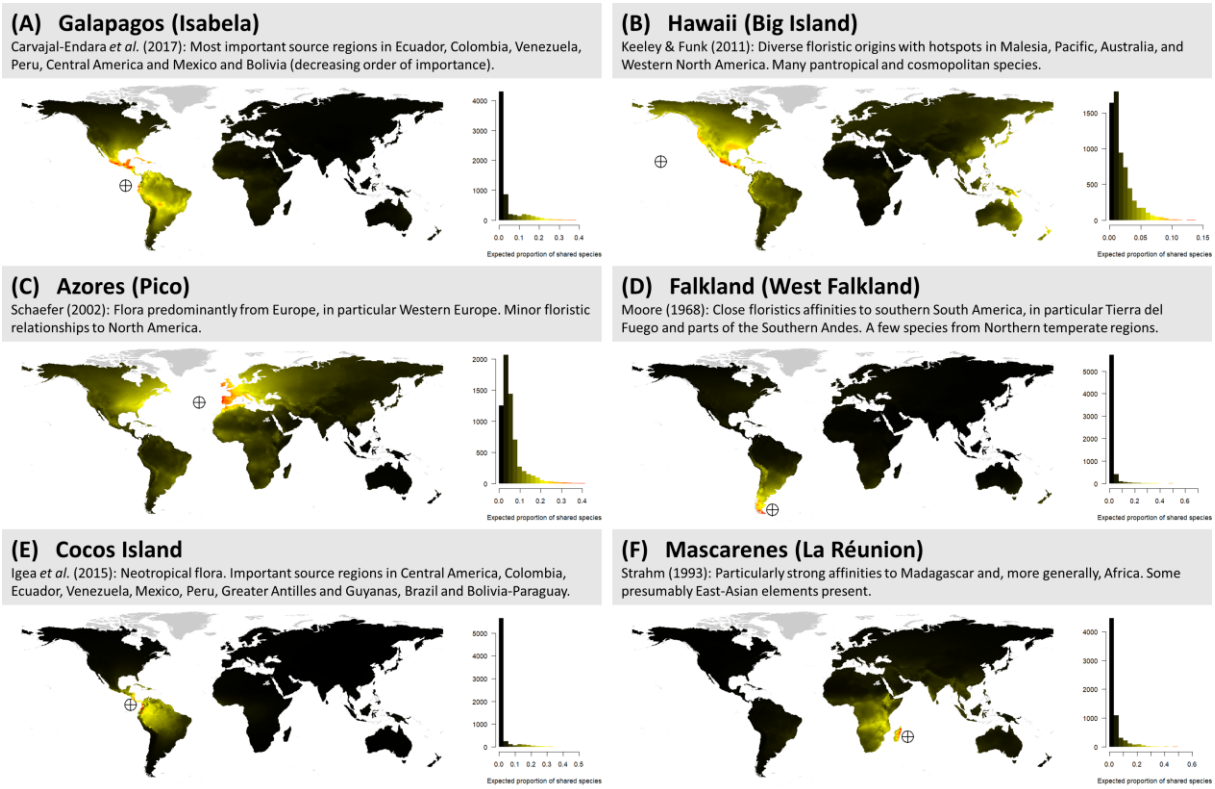

Figure 2: Exemplary comparison of empirically reconstructed and statistically modelled source regions for six islands. Grey boxes summarize the results of previous source region reconstructions based on floristic or phylogenetic affinities. Maps show corresponding statistical source region estimates (proportion of shared species, 1- β_{sim}) between the focal island and 6505 equal-area grid cells (~23,300 km² each). Predictions were derived from a generalized dissimilarity model (Ferrier et al. 2007) fitted with geographical and climatic characteristics of 611 mainland floras worldwide. Histograms show the distribution of predicted values for each focal island (note that the range of values differs among islands).

Our method for estimating island source regions showed strong agreement with empirical source region reconstructions (Figure 2). Accordingly, most island floras sample from a limited set of nearby and climatically similar mainland regions. The estimated source regions for the Falkland Islands, for instance, are highly concentrated in the nearby non-tropical parts of South America, which corresponds closely to the account given by Moore (1968) (Figure 2D). However, with increasing isolation from the mainland, the distribution of island source regions became more diffuse in both the statistical and empirical reconstructions. For example, we estimated the source regions of the Hawaiian flora to be Circum-Pacific (Figure 2B). While this wide distribution of source regions is generally in agreement with the empirical reconstruction Keeley & Funk (2011), our method puts more emphasis on North and Central America as source regions of the Hawaiian flora. Despite such minor discrepancies, the overall congruency between empirical reconstructions and our statistical estimates of island source regions demonstrates the robustness of our method.

Compositional and representational disharmony

Compositional disharmony (D_{comp}) ranged between 0.19 (Corsica, Mediterranean Sea) and 0.87 (Clipperton Island, East Pacific). Overall, the most harmonic island floras were found in the Mediterranean Basin and off the shores of temperate continental regions (East Asia, Europe, North America). Particularly disharmonic floras were located in the Arctic and Antarctic seas and the Central Pacific (Figure 3A). In agreement with our expectations, compositional disharmony increased with island isolation and decreased with island area (Table 1, Figure 3B). Although compositional disharmony differed strongly among island types (Figure 3B), geological origin (GEO) was not an important variable in the multi-predictor setting (Table 1); after controlling for the effect of island area, isolation and climatic characteristics, only atolls had a positive effect on D_{comp}. Correspondingly, none of most supported models included an interaction term. Climatic variables had consistently negative and unexpectedly strong effects on compositional disharmony. Measured by the slope standardized regression coefficients, precipitation seasonality (PVAR) was the second most important predictor of D_{comp} after area (AREA) – and before island isolation (DIST, Table 1). The explanatory power of geographical and climatic variables for compositional disharmony was relatively high ($R^2_{marginal} = 0.44$). However, the floras of e.g. Singapore (tropical, medium-sized shelf island, species-rich, not isolated, $D_{comp} = 0.45$) and South Georgia (Antarctic, large continental fragment, species-poor, highly isolated, $D_{comp} = 0.78$) indicate the existence of additional island-specific factors in creating compositional disharmony, which is also reflected by the substantial contribution of the random variable (ARCH) to the overall model fit ($R^2_{conditional} = 0.87$).

Table 1: Statistical model results for compositional disharmony (D_{comp}) and representational disharmony (D_{rep}).Variable abbreviations are given in the methods section. Variables are highlighted in bold if their confidence intervals (CI2.5, CI97.5) do not include zero.

Compositional disharmony (D_{comp})	Representational disharmony (D_{rep})

	estimate	std. error	$CI_{2.5}$	$CI_{97.5}$
Intercept	0.547	0.012	0.499	0.557
AREA	**-0.060**	0.005	-0.070	-0.051
DIST	**0.027**	0.009	0.009	0.046
MAT	-0.020	0.018	-0.058	0.000
TVAR	**-0.052**	0.015	-0.080	-0.024
MAP	**-0.025**	0.010	-0.045	-0.005
PVAR	**-0.027**	0.010	-0.047	-0.007
GEO	-			
Shelf	0	-	-	-
Fragment	-0.014	0.0230	-0.059	0.031
Floor	0.023	0.019	-0.015	0.061
Volcanic	0.015	0.014	-0.012	0.042
Atoll	**0.050**	0.022	0.007	0.093
model type	Gaussian Linear Mixed Effects Model			
variance explained	$R^2_{MARGINAL} = 0.44$ $R^2_{CONDITIONAL} = 0.87$			
sample size	320			

	estimate	std. error	p-value
Intercept	-0.307	0.279	0.272
AGE	-0.244	0.149	0.102
SPEC	**0.160**	0.027	< 0.001
GROUP	-	-	-
Angiosperms	-	-	-
Gymnosperms	0.073	0.200	0.714
Pteridophytes	**0.886**	0.113	< 0.001
model type	Gaussian Linear Model		
variance explained	$R^2 = 0.19$		
sample size	451		

Representational disharmony varied widely among vascular plant families (Figure 3C). Most notably, pteridophyte families were greatly over-represented on islands, whereas angiosperm and especially gymnosperm families tended to be under-represented. A few families such as Cycadaceae (gymnospermae, D_{rep} = 0.62) or Marsileaceae (pteridophytes, D_{rep} = -0.70) deviated from this general pattern. According to the multi-predictor model (Table 1), family species richness and taxonomic affiliation, but not family age had significant effects on representational disharmony. However, the explanatory power of the model was relatively low (R^2 = 0.19). Moreover, the relationship between family-level functional traits and representational disharmony was weak. Only in the case of pollination syndrome we found significantly higher values of D_{rep} for predominantly wind-pollinated families compared to predominantly insect-pollinated families (SI Figure 2). We did not find significant effects of growth form, self-compatibility, seed mass, fruit type and dispersal syndrome (SI Figure 2). In agreement with these results, we did not find a significant phylogenetic signal in D_{rep} for seed plants (C_{mean} = 0.05, p = 0.071), but only for all vascular plants including the strongly over-represented pteridophyte clade (C_{mean} = 0.16, p = 0.001, SI Figure 3).

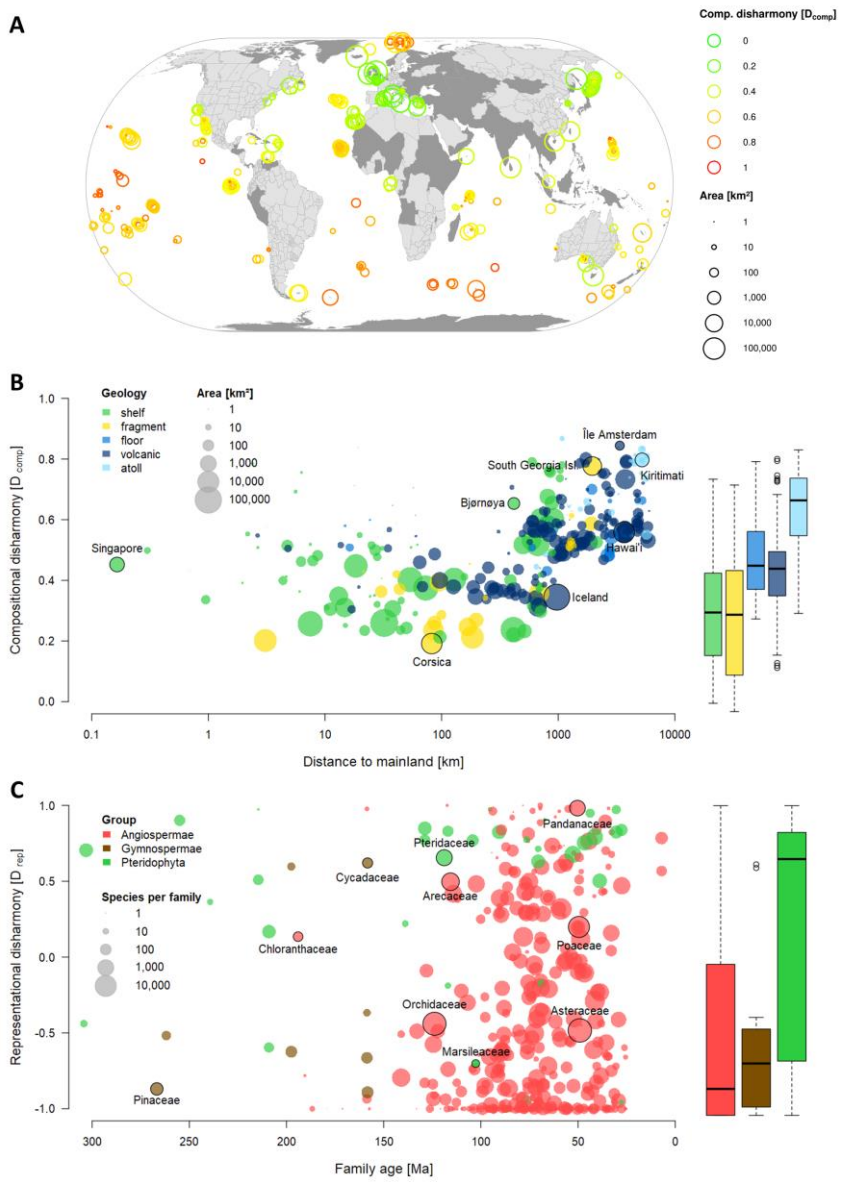

Figure 3: Global patterns in floristic disharmony from an island- and taxon-centred perspective. ***(A)*** *Compositional disharmony of island floras worldwide (n = 320). Mainland regions that were used for floristic comparisons (n = 611) are colored in light grey.* ***(B)*** *Compositional disharmony of island floras as a function of island isolation (x-axis), area (dot size), and geological origin (dot color). Higher values of D_{comp} indicate higher compositional dissimilarity relative to potential source regions on the mainland.* ***(C)*** *Representational disharmony of vascular plant families (n = 450) as a function of family age (x-axis), species per family (dot size), and taxonomic group (dot color). Values of D_{rep} above and below zero indicate a proportional over- and under-representation on islands, respectively.*

Discussion

Our results show that compositional disharmony is a common feature of island floras worldwide, and that the magnitude of this effect clearly depends on the classical biogeographical variables of isolation and area, but is modulated by climatic conditions and geological history of an island. We found less clear relationships between family-specific characteristics and representational disharmony, i.e. the proportional over- or under-representation of individual taxa on islands relative to the mainland. Here, the most important predictor variable was a simple categorization of families into angiosperms, gymnosperms and pteridophytes. In addition, species richness and pollination syndrome had significant effects on representational disharmony, whereas all other functional traits (growth form, dispersal syndrome, ability to self-pollinate, seed mass and fruit type) remained without effect.

One key innovation of the present study is the outlined method for estimating floristic source regions based on a statistical model of species turnover. Source regions are typically defined as discrete, relatively large geographical units such as continents, biogeographical regions or countries (Fosberg 1992; Keppel *et al.* 2009; Keeley & Funk 2011). This coarse-grained approach is often necessitated by the broad geographical scope of floristic data sources (e.g. regional checklists, inventories, Floras), but, nonetheless, has proven to be a valuable tool for understanding the origins of island floras. However, the recent explosion in ecological data availability (Hampton *et al.* 2013) has enabled more highly resolved, quantitative approaches to delineate source regions as biogeographical species pools (Carstensen *et al.* 2013). Currently, the most versatile methods are based on stacked distributions of individual species that are derived either empirically (Graves & Rahbek 2005) or from species distribution models (Karger *et al.* 2016). Such species-level approaches are theoretically well-suited for estimating source regions of a given island, but practically require complete knowledge on the spatial distribution of all species occurring there. At the moment, however, complete knowledge of global plant distributions is still beyond (Hortal *et al.* 2015). Our approach, in contrast, models the proportion of shared species directly, instead of generating it from a compilation of complex species-level information. Consequently, source region estimates based on species turnover are considerably less data-intensive than methods that require individual species distributions, while offering much finer spatial grain sizes and larger extents than empirical source region reconstructions (see Figure 2). Considering that for the majority of islands no quantitative estimates of floristic source regions are available, the proposed method might add valuable aspects to island biogeographical research.

Island colonization is an accumulative process, acting over millions of years. The extended temporal dimension introduces uncertainties to the estimation of island source regions because the climate, habitat distribution, position, size and shape of both islands (Whittaker *et al.* 2008; Weigelt *et al.* 2016) and source regions (Galley & Linder 2006; Pokorny *et al.* 2015) may have changed considerably since colonization. Cronk (1987) illustrates this for the flora of Saint Helena, which is mostly derived from a now-extinct wet forest flora that occupied large parts of Southern Africa during the Miocene. Moreover, the effective isolation of an island is difficult to quantify and depends not only on the distance to the mainland, but also on the availability of stepping stones and the direction of predominant sea and wind currents (Cook & Crisp 2005; Weigelt & Kreft 2013), as well as the dispersal abilities of the focal taxon. This is illustrated by the overestimated importance of Central American regions in our prediction of Hawaiian source regions (see Figure 2). Although Hawaii is situated closer to North America than to Asia and Australia, it is effectively less isolated from the latter continents because of interspersed Pacific islands that facilitate stepping-stone colonization (Carlquist 1967). Another potential source of uncertainty is that different habitats or elevational zones of an island may sample from distinct source regions on the mainland, and thus vary in their degree of isolation

(Steinbauer *et al.* 2012). A stronger consideration of the above-mentioned factors would certainly yield more accurate estimates of floristic source regions on the one hand, but adds much complexity on the other. Further methodological refinements and an extensive validation against empirical source region reconstructions may help to find the appropriate balance between complexity and utility.

Turnover-based estimates of species source regions may be applied to research questions beyond island disharmony. In conservation planning, for example, taxon-specific source region estimates could be derived from highly resolved distributional data such as vegetation plots or small-scale checklists to inform the design of regional ecological corridors and protected areas (Socolar *et al.* 2016). At larger scales, our approach could help to identify (potential) sources of species invasions and to implement measures preventing further introductions from such regions. Island conservation might particularly benefit from these tools, since island biotas are disproportionally affected by species introductions and naturalizations (van Kleunen *et al.* 2015; Bellard *et al.* 2016).

Dispersal filtering has long been regarded as the predominant process in the assembly of island biotas, and therefore the main driver of disharmony (Carlquist 1966, 1967). Our results reveal that this is only partly true. On the one hand, the strong effect of isolation on island disharmony indeed suggests a major role of dispersal filtering in removing less dispersive taxa from the set of potential colonizers of an island. All gymnosperms except for Araucariaceae and Cycadaceae were under-represented on oceanic islands, which seems to fit the classical notion of gymnosperms as poor dispersers. Likewise, pteridophytes – possessing superior long-distance dispersal capabilities via ultra-light spores – were found to be strongly over-represented in island floras. These findings are in line with previous studies, which interpreted these broad taxonomic patterns as the outcome of selective dispersal filtering (Kreft *et al.* 2010; Rumeu *et al.* 2014; Weigelt *et al.* 2015). On the other hand, the strong effects of area, temperature seasonality and geological origin, as well as the relationship between representational disharmony and pollination- but not dispersal-related traits, indicate an important role of non-dispersal related processes. Pollination is increasingly recognized as a critical factor for the colonization of islands (Olesen *et al.* 2010; Alsos *et al.* 2015; Grossenbacher *et al.* 2017). Given the general scarcity of animal pollinators on islands, abiotic pollination syndromes and the ability to self-pollinate are advantageous compared to biotic pollination or strict outcrossing (Baker 1955; Razanajatovo *et al.* in press). Indeed, we found wind-pollinated families to be much more evenly represented on islands than predominantly insect-pollinated families, whereas all other family-level traits had no detectable effects on representational disharmony. The lacking effect of classical dispersal traits such as seed mass, dispersal syndrome or fruit type seems to contradict longstanding assumptions regarding their relevance for island colonization (Carlquist 1974; Howe & Smallwood 1982; Portnoy & Willson 1993). Indeed, while a relationship between such traits and dispersal distance is evident at small scales up to

a few kilometers (Tackenberg *et al.* 2003), long-distance dispersal seems to operate with such high levels of stochasticity and complexity that this relationship vanishes (Higgins *et al.* 2003; Nathan 2006; Nogales *et al.* 2012). Moreover, many large-seeded species that are adapted to dispersal by birds or seawater are successful long-distance dispersers, defying the common notion of small seeds as indicator of good dispersibility. Other studies even find no relationship at all between dispersal traits and colonization success (Heleno & Vargas 2014).

Abiotic factors such as climate or soil substrate also act as filters for colonizing plant species, as recently demonstrated for the Galapagos Islands (Carvajal-Endara *et al.* 2017) and New Caledonia (Isnard *et al.* 2016). The strong effect of temperature-related variables in our analyses (Table 1) seems to support (abiotic) environmental filtering as an important driver of island disharmony. However, the climatic variables in our models did not reflect climatic similarity to the mainland (which would be a plausible cause of disharmony, but was accounted for during source region estimation), but the average conditions of the islands themselves. Potential explanations for the positive relationship between compositional disharmony and island temperature and temperature seasonality include (1) stronger environmental filtering on islands with temperate or polar climates, (2) higher speciation rates on warm tropical islands, or (3) glacial dynamics limiting the available time for colonization on cold, high-latitude islands. In addition, separating abiotic and biotic drivers of community assembly is often difficult because competitors may preclude the establishment of colonizing species in generally suitable habitats, thus creating artificial environmental gradients in the composition of communities (Kraft *et al.* 2015).

Even though the above considerations provide plausible explanations for the role of ecological factors in creating island disharmony, we want to stress that compositional disharmony, i.e. the overall compositional bias of island floras relative to their mainland source regions, is affected by neutral sampling effects related to species richness. Island floras can never be a perfect compositional representation of the much larger pool of mainland species, because the number of families on an island is constrained by the number of species. Thus, extremely small proportions that arise, for example, in the case of rare families in species-rich mainland floras cannot be reproduced on islands, which inevitably increases compositional disharmony with decreasing species number (SI Figure 4). This interpretation moreover implies that compositional disharmony is also dependent on the size and spatial extent of the mainland source pool, as larger source pools usually include a higher number of taxa and are thus less likely to be represented harmonically in an island flora. This dependency might provide a further piece in the puzzle of understanding the disharmonic floras of highly isolated islands such as Hawaii or the Azores (see Figure 2B,C), whose source regions often encompass different biogeographical regions and continents.

If the overall bias of island floras is rather accurately predicted by geographical and climatic island features, why does the representation of individual families on islands seem so unrelated to their functional traits? We consider two aspects relevant here. First, we approximated family-level traits based on species-level information of varying completeness (SI Figure 2). Missing data is a common problem in trait-based ecology (Taugourdeau *et al.* 2014; Penone *et al.* 2014) and a major source of uncertainty and bias in the characterization of ecological patterns (Hortal *et al.* 2015). We therefore caution that our findings on representational disharmony depict trends rather than a definitive assessment. Second, a taxonomic perspective – especially when focussing on a fixed taxonomic level – is not an ideal framework for examining the outcomes of the complex ecological processes that produce disharmonic island floras. In the scientific literature, examples of disharmonic floristic elements range from small genera (e.g. *Metrosideros* in Carlquist 1966) to large taxonomic clades (e.g. pteridophytes in Braithwaite 1975). Some studies assemble several such examples for a particular island or island group in order to arrive at a more general conclusion (Carlquist 1967; Whittaker *et al.* 1997). In fact, this is a reasonable approach because the degree to which taxa are consistently over- or under-represented on islands depends on their uniformity in terms of colonization success, and thus in terms of dispersal abilities, environmental tolerances and degree of biotic specialization. These parameters may vary greatly even within small families (Howe & Smallwood 1982), but on the other hand show remarkable consistency within large taxonomic groups (Farjon 2010), such that the required taxonomic level of observation is variable. Consequently, the classical concept of island disharmony *sensu* Carlquist *(1965, 1974)* – albeit immensely useful and influential – generalizes poorly across taxonomic groups.

We demonstrated that island disharmony is a common feature of insular floras worldwide, and that the traditional concept can be put on a quantitative footing. The generality and predictive power of the concept of island disharmony has historically been limited by its focus on taxonomic categorizations. However, given the rapid advances in ecological data availability and analytical tools, the approximation of ecological characteristics by means of taxonomic affiliation will eventually become obsolete. Instead, the assembly mechanisms that disharmony aims to reflect and explain can be investigated more directly using quantitative methods that are informed by functional and phylogenetic data. The outlined approach for the estimation of island source regions as well as the mathematical indices for quantifying island disharmony provide a big step towards this objective, and offer robust empirical insights into the factors shaping the composition of island floras.

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