ECOGRAPHY

Research

Island area and historical geomorphological dynamics shape multifaceted diversity of barrier island floras

Thalita Ferreira-Arruda, Nathaly R. Guerrero-Ramírez, Pierre Denelle, Patrick Weigelt, Michael Kleyer and Holger Kreft

T. Ferreira-Arruda (https://orcid.org/0000-0003-1385-0226) ✉ (thalita.ferreira-arruda@uni-goettingen.de), N. R. Guerrero-Ramírez (https://orcid.org/0000-0001-7311-9852), P. Denelle (https://orcid.org/0000-0002-4729-3774), P. Weigelt (https://orcid.org/0000-0002-2485-3708) and H. Kreft (https://orcid.org/0000-0003-4471-8236), Biodiversity, Macroecology and Biogeography, Univ. of Göttingen, Göttingen, Germany. PW and HK also at: Center of Biodiversity and Sustainable Land Use, Univ. of Göttingen, Göttingen, Germany. PW, Campus-Inst. Data Science, Göttingen, Germany. – M. Kleyer (https://orcid.org/0000-0002-0824-2974), Inst. of Biology and Environmental Sciences, Univ. of Oldenburg, Oldenburg, Germany.

The influence of island dynamics and characteristics on taxonomic diversity, particularly species richness, are well studied. Yet, our knowledge on the influence of island dynamics and characteristics on other facets of diversity, namely functional and phylogenetic diversity, is limited, constraining our understanding of assembly processes on islands (e.g. biogeographic history, dispersal and environmental filtering and species interactions). Using barrier islands, a highly dynamic and so far, understudied island type, we investigate how multiple facets of vascular plant diversity (functional, phylogenetic and taxonomic diversity) are shaped by island geomorphology, modern and historic area, and habitat heterogeneity. In line with our expectation, historical dynamics in island geomorphology affected phylogenetic and taxonomic diversity via habitat heterogeneity. However, island area was the best predictor across all facets of diversity. Specifically, larger islands had higher functional and phylogenetic diversity than expected by chance while most of the smaller islands had lower diversity. The influence of area on functional diversity acted via habitat heterogeneity, with habitat heterogeneity influencing negatively functional diversity. Our results suggest that larger islands accumulate functionally and phylogenetically unique species. Further, results for functional diversity pointed towards potential area–heterogeneity trade-offs, with these trade-offs likely resulting from increased interspecific competition favoring a specific set of trait values (of stronger competitors), particularly on smaller islands. Together, these results demonstrate that going beyond taxonomic diversity contributes to identifying underlying processes shaping diversity–area relationships.

Keywords: functional diversity, island biogeography, habitat heterogeneity, phylogenetic diversity, species–area relationship

1

Introduction

In search of answers to complex ecological and biogeographical questions, scientists have long turned to islands as model systems (Warren et al. 2015) due to their comparatively small size, distinct spatial boundaries and their striking examples of evolutionary diversification (Mayr 1963, Losos and Ricklefs 2010). Island research has advanced our general understanding of evolutionary and ecological patterns and processes reaching far beyond islands, including the species–area relationship (Rosenzweig 1995, Triantis et al. 2012), the role of immigration and extinction (MacArthur and Wilson 1967) and adaptive radiation (Gillespie and Roderick 2002, Kisel and Barraclough 2010). One of the most prominent outcomes of island research, the equilibrium theory of island biogeography (ETIB) by MacArthur and Wilson (1967), points to area and isolation as the major aspects influencing species richness on islands. However, test of ETIB found that other aspects such as climate (Kreft et al. 2008), environmental heterogeneity (Barajas-Barbosa et al. 2020), geodynamics and disturbance history (Fahrig et al. 1993, Weigelt et al. 2016) as well as island age (Whittaker et al. 2008) also greatly influences insular plant diversity.

Island area is probably the most well studied abiotic island feature and its relationship with species richness is well known as the species–area relationships (SAR) (Turner et al. 2005, Triantis et al. 2012). Beyond being influenced by factors such as spatial scale, sampling, minimum area effects and geographical location (Turner et al. 2005), the SAR also reflects underlying ecological processes, as higher habitat heterogeneity and increasing immigration and speciation rates (Connor and McCoy 2001, He and Legendre 2002). Habitat heterogeneity is, arguably, the most consistent factor influencing SAR, from local to global scale (Rosenzweig 1995, Turner et al. 2005). However, the relationship between area and habitat heterogeneity is not always straightforward. When heterogeneity increases for a given area, the effective area available for species is reduced which in turn may lead to declines in population size (Allouche et al. 2012, Ben-Hur and Kadmon 2020). However, such a hump-shaped relationship between species richness and habitat heterogeneity might not apply to island systems (Hortal et al. 2009). Despite extensive research, disentangling the effects of area and habitat heterogeneity on biodiversity remains an important task, and going beyond species taxonomic identity might shed light on how those two aspects are intertwined.

Although area and habitat heterogeneity are paramount for our understanding about island biodiversity, they do not capture island dynamics. Recent models in island biogeography highlight the importance of geo-environmental dynamics for key ecological processes like immigration, speciation and extinction and ultimately biodiversity dynamics on islands (Heaney 2000, Whittaker et al. 2008). Such non-equilibrium models stress that island age and geological ontogeny affect the carrying capacity of islands through time (Whittaker et al. 2008). Island dynamics are present across a wide range of spatial–temporal scales, and range from tidal dynamics that shape island coastlines and coastal communities on a daily basis, wave action and sedimentation that change island area at the scale of decades and centuries (Fitzgerald et al. 1984, Ernstsen et al. 2006) as well as changes in climate and sea levels due to glacial cycles over tens of thousands of years (Weigelt et al. 2016) and geological dynamics over millions of years affecting species turnover, immigration and extinction rates (Whittaker et al. 2008).

The effects of area, habitat heterogeneity and island dynamics on other biodiversity facets than species richness is poorly understood (Matthews et al. 2015, 2020, Negoita et al. 2016). For a more mechanistic understanding of community assembly processes and how they influence biodiversity patterns at different scales (Leibold and Chase 2018), we should consider the interrelationships between the three primary facets of biodiversity: taxonomic, functional and phylogenetic diversity (Latham et al. 1993, Swenson 2011, 2014, Bauer et al. 2021). Functional diversity represents the variation in morphological, physiological and ecological traits that affect individual performance and fitness (Garnier et al. 2016), which in turn can help explain ecological strategies and assembly processes (Tilman 2013). Studying traits variation related to species dispersal and resource acquisition strategies may unveil the main dispersal and environmental filters (Kraft et al. 2015a, de Bello et al. 2021). Phylogenetic diversity represents the phylogenetic relatedness among species in a community that can be used to investigate assembly processes and the role of species interactions (Faith 1992, Webb et al. 2002).

Research on the influence of spatial features on functional and phylogenetic diversity has found highly context-dependent relationships. For instance, Mazel et al. (2014) and Jarzyna and Jetz (2018) showed that richness-based metrics of functional and phylogenetic diversity produce a similar pattern as taxonomic diversity. However, the functional diversity–area relationship (FDAR) has a lower saturation point (i.e. when functional diversity stops increasing with area and the FDAR curve stabilizes) than SAR, indicating functional redundancy, i.e. several species with similar trait values, while the number of species still increases. In contrast, Karadimou et al. (2016) did not find evidence of a saturation point of FDAR. Wang et al. (2013) found that FDAR as well as phylogenetic diversity–area relationship (PDAR) closely mirrored SAR, but FDAR and PDAR did show scale dependency, indicating competitive exclusion at small scales and habitat filtering at larger scales. Zhang et al. (2021) showed an area threshold requirement to maintain functional diversity of woody plants. Overall, there is still a knowledge gap when it comes to understanding the scale dependency of functional and phylogenetic diversity.

A large proportion of studies in island biogeography focuses on oceanic islands (e.g. islands of volcanic origin such as the Hawaiian and Canary Islands or Galápagos), but other island types with different ontogenies and geo-environmental dynamics can offer fresh perspectives in island biogeography (Ali 2017). Barrier islands, for instance, have highly dynamic landscapes composed mainly of unconsolidated

sediments (Davis 1994, Wang and Roberts Briggs 2015). These highly dynamic landscapes suffer from plant biomass destruction by stochastic disturbances in addition to large variation in resource availability over a short period of time; processes that may break established environment–plant–ecosystem relationships (Kleyer et al. 2014). Studies on rivers and wetlands found that neutral processes and dispersal limitation better explain species diversity in highly dynamic ecosystems than environmental filtering (Isabwe et al. 2019, Schöpke et al. 2019).

Barrier islands occur along about 15 percent of the world's coasts and are present on almost all continents (Davis 1994). Constant geomorphological activity caused by wind and water are changing barrier islands by destroying and renewing features across various temporal and spatial scales. While past geographical conditions and temporal changes in environmental conditions are increasingly recognized to greatly influence present plant diversity on oceanic islands (Whittaker et al. 2008, Warren et al. 2015, Weigelt et al. 2016), their role in determining plant diversity of barrier islands remains largely unexplored. Water-related mechanisms shaping barrier islands can be explained by inlet sediment bypassing, where sand is carried out from the beach by longshore drift and deposited at the upstream, as the inlet erodes the downstream causing the islands to move (Fitzgerald et al. 1984). Therefore, all barrier islands share 'head' and 'tail' as common elements (Oost et al. 2012). In the Frisian islands, this process happens mainly from west to east following the direction of the sea tides and strong wind; that way the western parts of the islands (representing the 'head') consist of older, more consolidated sediment, while the islands' 'tail' in the east are the younger parts of the islands, made up of newer sediments. The island tail mainly consists of salt-marshes and dunes and their extent vary widely from island to island (Groot et al. 2017). The West and East Frisian are much younger than most oceanic islands and thus lack in-situ diversification and endemic species (Niedringhaus et al. 2008).

Here, we investigate how different facets of plant diversity are affected by area (modern and historic), habitat heterogeneity and island geomorphological dynamics. The Frisian Islands are a particularly interesting model system to study the impact of island features on multifaceted diversity, because of their fast-changing geomorphology and constant environmental disturbances. They offer an opportunity to gain insights into patterns and drivers of biodiversity in a highly dynamic island system with geomorphological dynamics acting at the decadal to centennial time spans. The geomorphology of the Frisian islands causes them to grow by increasing the island's 'tails', where habitats are mainly salt marshes and dunes. Therefore, we expect that the increase in island area will not necessarily amount to the increase in habitat heterogeneity. Consequently, larger islands can have a larger number of species, but species will remain highly similar in their functional traits. We hypothesize that 1) habitat heterogeneity positively affects functional and phylogenetic diversity, and that it is a stronger

predictor than area per se. Considering the constant disturbances naturally present in the barrier island system, we also hypothesize that 2) the temporal geomorphological dynamics negatively impact functional, phylogenetic and taxonomic diversity either directly or via changes in area and habitat heterogeneity.

Material and methods

Study site

The West and East Frisian Islands are located at the coastline of Germany and the Netherlands in the North Sea (53°02′05″N, 4°43′35″E–53°47′08″N, 8°00′20″E) (Fig. 1). This chain of barrier islands comprises 17 islands, all of which originated from sedimentation and erosion processes (Streif 1989, Homeier et al. 2010) with the exception of Texel which became disconnected from the mainland in the 12th century by the 'All Saints' flood (Eisma and Wolff 1980). The islands vary in size (Table 1) and usually have an elongated shape, oriented parallel to the shore line; they are of similar age and at a similar distance from the shore (7 km on average). Most of the Frisian islands were formed approximately 7000 years ago when large amounts of sand accumulated along the seashores by tidal action, creating dune ridges. Subsequently, plant colonization led to the stabilization of those dunes and the formation of salt marshes (Streif 1989, Davis 1994).

Species distribution

We extracted species distributions of vascular plants for each island from two different sources: Niedringhaus et al. (2008) for the East Frisian Islands and the Nationale Databank Flora en Fauna (2015) for the West Frisian Islands. The East Frisian comprised a group of ten islands with 1004 species, the West Frisian had a total of seven islands and 1368 species. We first standardized species' names according to The Plant List, (2010). Hybrids and infra-specific ranks were excluded. During name standardization, 69 species names were changed in the East Frisian dataset and 161 in the West Frisian dataset. Since all Frisian Islands are modified by human land use, we filtered out non-native species (Tamis et al. 2004, Niedringhaus et al. 2008) to best represent natural patterns. We then filtered out species known to only occur in human-dominated habitats as classified by Klotz and Durka (2002) and Niedringhaus et al. (2008), assuming that even though native, these species would not be capable of colonizing the islands without human interference. From that we obtained a total of 938 species on East Frisian and West Frisian.

Functional traits and phylogenetic information

We selected four traits that represent different ecological strategies (Díaz et al. 2016): 1) maximum plant height (m), is connected to light interception and seed dispersal facilitation (Moles et al. 2009, Garnier et al. 2016); 2) seed mass
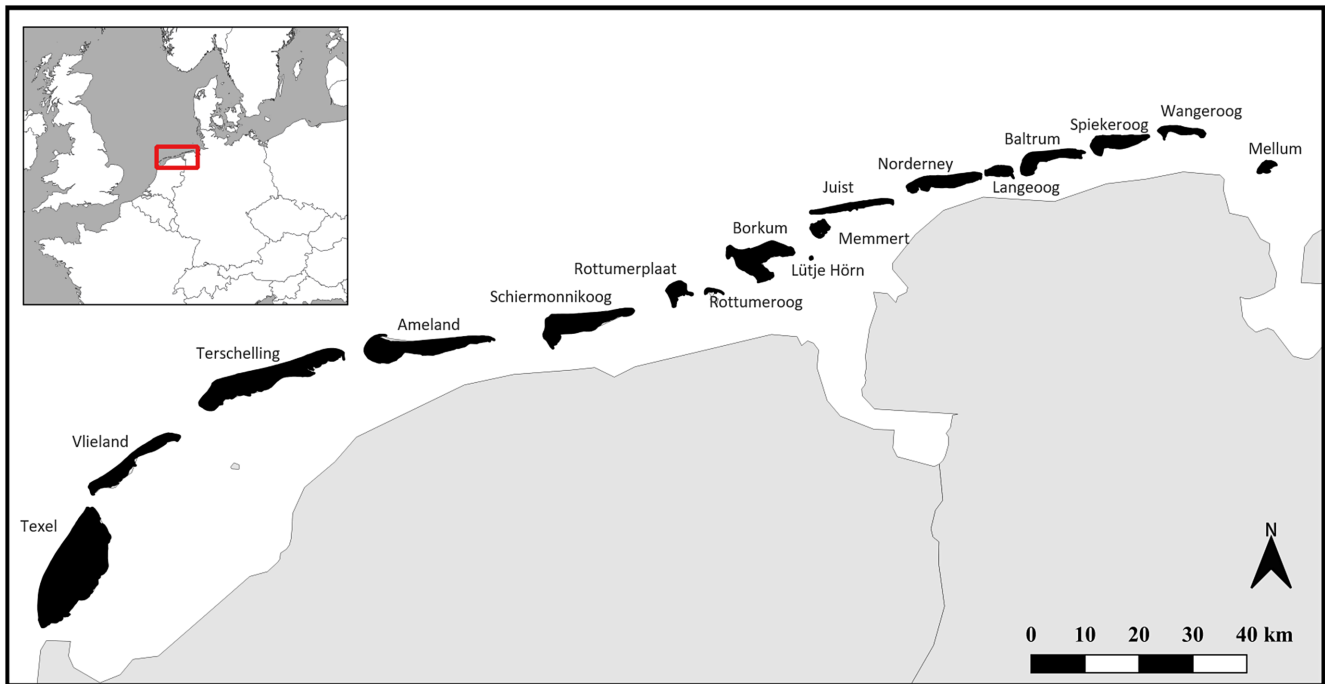
Figure 1. Map of the study area showing the 17 West and East Frisian Islands located off the German and Dutch coastline in the North Sea.

(mg) is linked to colonization capacity and seedling survival (Thompson et al. 1993, Moles et al. 2004, Wyse and Hulme 2021); 3) leaf mass per area (g cm^{-2}) is related to carbon gain and leaf life span (Wright et al. 2004, Poorter et al. 2009); 4) leaf area (mm^2) is linked to leaf energy production and water balance (Ackerly and Donoghue 1998, Farquhar et al. 2002). We obtained trait data primarily from the LEDA Traitbase (Kleyer et al. 2008), as the trait data salt marshes and dunes were collected in the East Frisian islands and further complemented them with data from Minden et al. (2012), Minden and Kleyer (2015) and Kleyer et al. (2019). Further missing trait information was extracted from the GIFT (Weigelt et al. 2020) and TRY databases (Kattge et al. 2020). We standardized trait values to the same units of measurement and if species had more than one measurement for the same trait, we took the mean, except for maximum plant height where we took the 90th percentile, in order to preserve the highest values. We only considered species with data for at least three out of the four traits, reducing our data set to a total of 712 species. From the 712 species, 99% had available data for maximum plant height, seed mass and leaf mass per area, while only 79% had data for leaf area. We imputed the remaining missing trait values using the missForest function in the *missForest* package (Stekhoven and Bühlmann 2012) which imputes missing values by repeatedly fitting a random forest (Breiman 2001) on the observed part of each plant trait. It uses phylogenetic eigenvectors (n = 1–30) to reduce prediction error, by selecting the number of phylogenetic eigenvectors that had the minimum imputation error for each trait. For the phylogenetic information we used the Daphne phylogenetic tree by Durka and Michalski (2012).

Multifaceted diversity

Taxonomic diversity is defined by species richness of each island. We assessed functional diversity as functional richness, using the hypervolume approach proposed by Blonder (2018), which places each species of an island within a multidimensional trait space and quantifies functional richness as the total volume created by all species in the trait space. Hypervolumes rely on kernel density estimations based on the distributions of the observations which returns a volume in a multidimensional space accounting for holes, i.e. missing trait combinations. To make sure the hypervolume for each island was comparable among each other and to identify structuring axes that segregate species, we performed principal component analysis (PCA) of the traits for the total species pool and used the first three axes of this PCA as our dimensions for the calculation of hypervolume and kernel bandwidth estimation, using Silverman's rule (Silverman 1986). Kernel bandwidth and hypervolume were calculated using the functions estimate_bandwith and hypervolume from the R package *hypervolume* (Blonder et al. 2014).

To assess phylogenetic diversity, we used the richness-based metric Faith's phylogenetic diversity (Faith 1992), calculated by summing up the branch lengths of the species (Tucker et al. 2017). We calculated Faith's phylogenetic diversity based on a matrix containing presence and absences of native species in each island and in our constructed tree using the function pd from the package *picante* (Kembel et al. 2010). Because functional and phylogenetic diversity systematically increase with species richness we standardized both values for effect size. Effect size control for species richness by testing for

Table 1. Island names and their respective geomorphological dynamics defined by the coefficient of variation of island area between 1700 and 2008. Habitat heterogeneity calculated as the Shannon index of different habitat area proportions. The total area and historic area in km². Functional diversity shown as observed (OBS) and standardized (SES) values. Phylogenetic diversity shown as observed (OBS) and standardized (SES) values. Taxonomic diversity refers to the absolute number of species on each island. Note that Lütje Hörn does not have data for its habitats in the Ecosystems types of Europe database, hence a value of habitat heterogeneity is missing.

| | Island characteristics | | | | Plant diversity | | | | |
| | | | | | Functional | | Phylogenetic | | Taxonomic |
Island	Geomorphological dynamics	Habitat heterogeneity	Area	Historic area	OBS	SES	OBS	SES	OBS
Ameland	0.29	2.97	47.7	55.1	22.6	0.7	484	1.1	484
Baltrum	0.49	2.79	3.72	7.36	17.9	−1.8	317	−23.7	317
Borkum	0.27	4.15	24.83	19.04	19.1	−2.2	442	−15.2	442
Juist	0.17	3.3	8.83	11.7	19.4	−1.7	394	−24.3	394
Langeoog	0.33	5.17	14.18	9.83	18.7	−2.1	367	−13.1	367
Lütje Hörn	0.22	–	0.06	1.62	12.5	−0.7	44	−46.6	44
Mellum	0.43	1.37	2.11	2.78	17.2	−1.5	205	−55.6	205
Memmert	0.44	1	1.06	3.62	15.3	−2.6	217	−39.3	217
Norderney	0.33	4.4	18.06	11.98	18.2	−2.4	397	−21.4	397
Rottumeroog	0.59	1.14	1.06	8.57	13.3	−2.1	110	−49.7	110
Rottumerplaat	0.25	2.03	6.34	6.22	16.8	−0.7	114	−32.2	114
Schiermonnikoog	0.40	3.45	36.62	18.74	21.8	−0.1	449	−11.6	449
Spiekeroog	0.05	3.21	15.35	7.44	19.4	−1.1	323	−24.1	323
Terschelling	0.28	3.48	72.97	65.71	23.2	1.2	555	−6.2	555
Texel	0.35	2.75	92.97	99.13	22.4	0.3	597	7.1	597
Vlieland	0.23	3.72	31.59	59.35	22.1	0.2	424	5.2	424
Wangerooge	0.09	2.9	3.50	8.28	18.6	−1.7	351	−22.7	351

significant deviation between observed and random communities. Therefore, it can inform if functional and phylogenetic diversity are higher or lower than expected by chance for a given species richness. We ran 100 null models, reshuffling the species list of each island from the total species pool, and then calculated the standardized effect sizes (SES) for functional and phylogenetic diversity, using the formula as follows: SES = (obs. value − null mean)/null standard deviation; where 'SES' is standardized diversity index; 'obs. value' is the observed diversity index, while 'null mean' and 'null standard deviation' are the mean value and standard deviation of the null distribution of diversity index values generated for each island (Gotelli and Graves 1996). SES values lower than zero indicate less diversity than expected by chance, given species richness, while positive values indicate higher diversity than expected. However, since SES usually leads to a normal distribution of data, significance starts at the 5% margin (above and below (−)1.96) (de Bello et al. 2021). Functional and phylogenetic diversity were highly correlated with taxonomic diversity (r = 0.77 and r = 0.97, respectively). Null model standardization reduced the correlation among functional and phylogenetic diversity with taxonomic diversity to r = 0.26 and r = 0.75, respectively (Supporting information).

Abiotic island features

We extracted habitat heterogeneity from raster files at 100 m resolution from the Ecosystem Types of Europe dataset (Weiss and Banko 2018) (Supporting information), which maps 18 different habitats on the Frisian Islands. We excluded habitats classified as urban or anthropogenic (n = 6 habitats). Then, we calculated the effective number of habitats based on their area using the Hill number approach (Chao et al. 2014), with total number of habitats (Hill number q = 0), Shannon diversity (Hill number q = 1) more strongly weighting rare habitats, and Simpson diversity (Hill number q = 2) more strongly weighting common habitats. Patterns were consistent when including total number of habitats, Shannon or Simpson diversity; we thus focus on results for the effective number of habitats with q = 2 (Simpson diversity). We calculated the effective number of habitats for each island except Lütje Hörn for which no data were available regarding its habitat types. Island area was assessed in two different ways: First, modern island area (hereafter area) was quantified by summing the area of natural and semi-natural habitats occurring for each island. Second, historic area was based on the year 1700 for all islands except Rottumerplaat (with the oldest record from 1900). To assess temporal geomorphological dynamics, we followed the approach by Scherber et al. (2018) using temporal area variation as a proxy for geomorphological dynamics. Temporal area variation serves as a proxy for the geomorphological dynamics of the islands because the changes in area are a consequence of the geomorphological processes of sedimentation and erosion caused by the tides and strong winds as well as big catastrophic events like floods and storms. We retrieved past island area from different points in time ranging from 1700 to 2008, from geo-referenced historical maps using QGIS (QGIS Development

Team 2020) and calculated the coefficient of variation (standard deviation divided by the mean) (Table 1). East Frisian islands historical maps are from Homeier et al. (2010)) and historical maps of West Frisian island are from Utrecht Univ. library special collections: maps and atlases and David Rumsey map collection (Supporting information).

Statistical analyses

Due to the lack of consensus on which model form provides the best fit to FDAR and PDAR, we fitted 12 different models and averaged them (Mazel and Thuiller 2020). The models were weighted according to their AIC values and we further derived the average SAR, and standardized FDAR and PDAR. Using the R package 'sars' (Matthews et al. 2019), we started with the 20 models available in the package and evaluated the model's normality of the residuals by Shapiro–Wilk tests and used Pearson correlation between squared residuals and area to test for homoscedasticity. The models that passed the tests were used for the final averaged diversity–area curves.

To assess the influence of island dynamics, area and habitat heterogeneity on the diversity facets, we used piecewise structural equation models (SEM) using the approach proposed by Lefcheck (2016). SEMs link multiple response and predictors variables in a single causal network, relying on pre-existing knowledge of the system to make educated hypotheses on the causal relationships between variables (Shipley 2016). It allowed us to test a hypothetical causal model based on a priori knowledge related to the relationships between island dynamics, area and habitat heterogeneity. We established two alternative SEM, one using area and another using historic area (Fig. 2a, b) For the SEM using area, direct paths between
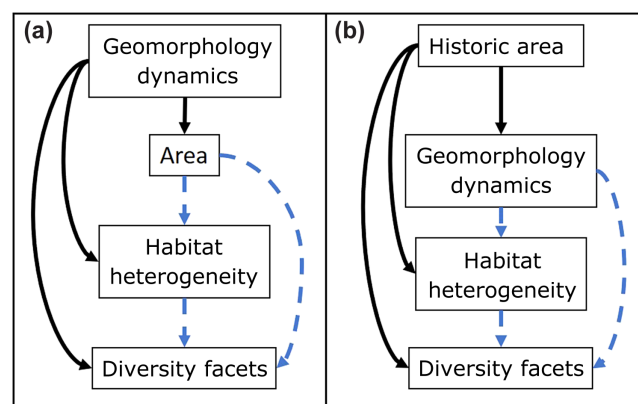

Figure 2. Conceptual figure of two alternative structure equation models on how modern and past island characteristics might affect different facets of insular plant diversity. Solid lines are the initial path added in the model while dotted blue lines were added only if this improved the model fit (based on modification indices, p-value < 0.05). In panel (a), geomorphological dynamics are hypothesized to influence diversity facets directly or indirectly via area and/or habitat heterogeneity. Alternatively, in panel (b), historic area is hypothesized to influence diversity facets directly or indirectly via geomorphological dynamics and/or habitat heterogeneity.

geomorphological dynamics and area, geomorphological dynamics and habitat heterogeneity and island dynamics and diversity facets were included in the initial model. Alternative paths to the initial model between area and habitat heterogeneity as well as them and the biodiversity facets were added, if this improved the model fit (based on modification indices, p-value < 0.05, Fig. 2a). For the SEM using historic area, direct paths between historic area and geomorphological dynamics, historic area and habitat heterogeneity and historic area and diversity facets were included in the initial model. Alternative paths to the initial model between geomorphological dynamics and habitat heterogeneity as well as them and the biodiversity facets were added, if this improved the model fit (based on modification indices, p-value < 0.05, Fig. 2b). Area (and historic area) and habitat heterogeneity were both log-transformed to fit normal distribution. Model fits were assessed using Fisher's *C* statistic based on the test of directed separation. Therefore, if the p-value of the test was > 0.05, we considered the data to fit the hypothetical causal network (Lefcheck 2016). To calculate the piecewise SEM, we used the function psem from the *piecewiseSEM* package (Lefcheck 2016). We also did a sensitive analyses on a data subset using two more traits, stem specific density to assess growth strategy and mechanical resistance (Díaz et al. 2016) and leaf nitrogen per leaf area, an indicator of the photosynthetic potential and herbivory resistance (Chapin 1980, Diaz et al. 2004).

Results

PCA of species traits revealed two independent main components that together accounted for 68% of the variation in the four-dimensional trait space. Plant height and seed mass were mostly associated with PC1 (42.6%) while leaf traits contributed mostly to PC2 (24.8%) (Supporting information). Most species were short stature, had small seeds and relatively acquisitive leaf strategy, i.e. low leaf mass per area. Most of the islands showed underdispersion (negative values) for standardized functional diversity (hereafter FD.ses) and standardized phylogenetic diversity (hereafter PD.ses) (Table 1). Larger islands had FD.ses values close to zero, indicating randomness, or above it, indicating overdispersion of traits. Underdispersion in FD.ses was more pronounced in islands with area size below 30 km². Texel, the largest island with the highest taxonomic diversity, had lower FD.ses than Terschelling and Ameland, that are considerably smaller and have less habitat heterogeneity. In the case of PD.ses, all islands showed values departing from the null expectations, however only three islands showed PD.ses values above zero (Texel, Vlieland and Ameland). Contrary to FD.ses, PD.ses does not show an area threshold, where the patterns change from underdispersion to overdispersion. The FDAR curve (Fig. 3a) showed a linear form, while he PDAR (Fig. 3b) curve mirrored the one of SAR (Fig. 3c).

Geomorphological dynamics measured as the coefficient of variation in island area varied from 0.05 to 0.59, Moreover, geomorphological dynamics were unrelated to island area
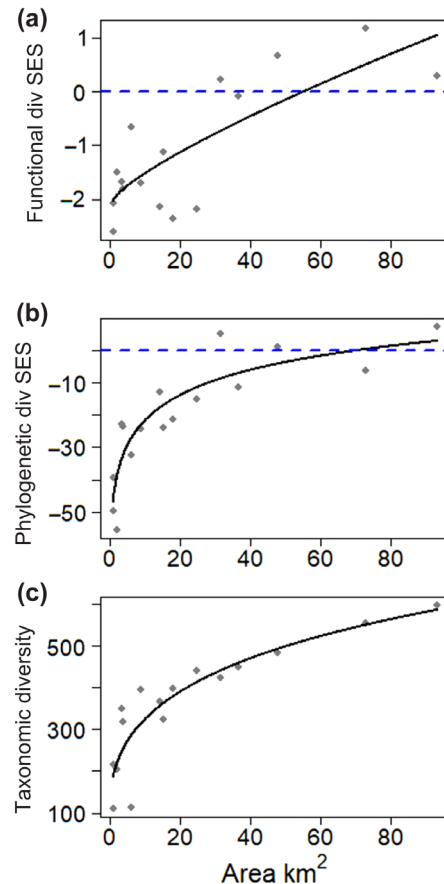

Figure 3. The three facets of diversity and their area relationship. Dashed blue lines in (a) and (b) mark the 0 point value. Values below 0 indicate functional and phylogenetic diversity lower than expected by chance (underdispersion); and values above 0 indicate functional and phylogenetic diversity higher than expected by chance (overdispersion).

with the whole range of values of geomorphological dynamics covered in smaller islands (Fig. 4a). In contrast, geomorphological dynamics negatively influenced habitat heterogeneity, as islands with lower geomorphological dynamics presented higher habitat heterogeneity (Fig. 4b). Further, larger islands were associated with higher habitat heterogeneity (Fig. 4c). Additionally, linear models results showed that standardized FD.ses was neither influenced by habitat heterogeneity (Fig. 5a) nor by geomorphological dynamics (Fig. 5b), PD.ses was positively influenced by habitat heterogeneity (p < 0.0001, r²=0.51) (Fig. 5c) but not by geomorphological dynamics (Fig. 5d). Taxonomic diversity was positively influenced by habitat heterogeneity (p < 0.0001, r²=0.47) (Fig. 5e) but not by geomorphological dynamics (Fig. 5f).

When analyzing the relationships by piecewise SEMs, area explained 74, 80 and 78% of the variance for FD.ses, PD.ses and taxonomic diversity, respectively; with area driving the variation across diversity facets either directly (standardized effects=1.2, 0.88 and 0.78 for FD.ses, PD.ses and taxonomic diversity, respectively) or via habitat heterogeneity (standardized effect via habitat heterogeneity=−0.47 for FD.ses,
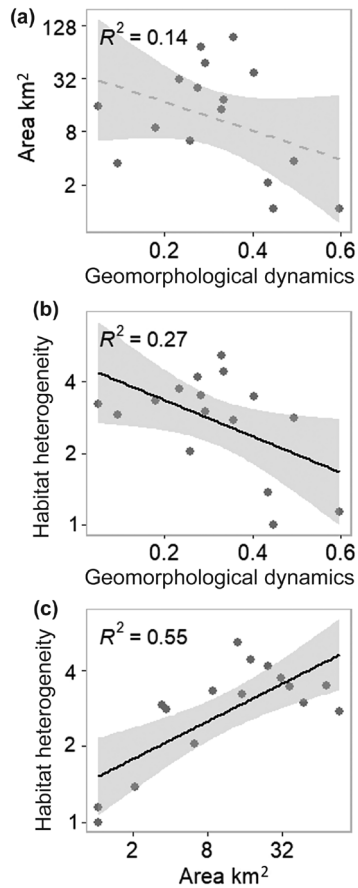
Figure 4. The three abiotic factors and their relationships. Solid lines indicate significant relationships (p < 0.05) and dashed lines show non-significant ones. Confidence intervals are shown as gray contours. When analyzed individually geomorphological dynamics presented no significant relationship with area but a negative relationship with habitat heterogeneity.
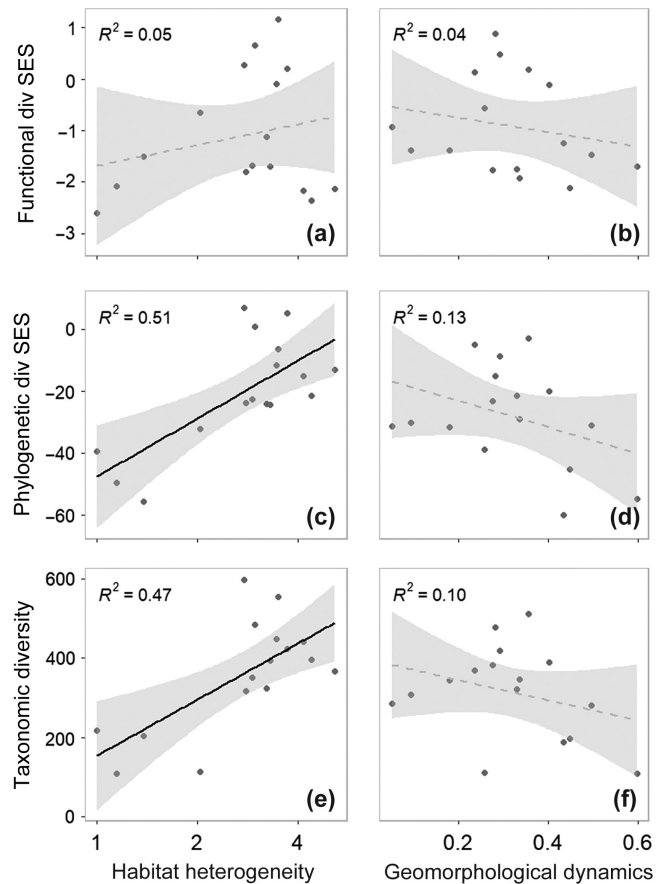

Figure 5. The three facets of diversity and their correlation with habitat heterogeneity and geomorphological dynamics. Solid lines indicate significant relationships (p < 0.05) and dashed lines show non-significant ones. Confidence intervals are shown as gray contours. When analyzed individually neither habitat heterogeneity nor geomorphological dynamics showed correlation with FD.ses (a), (b). Habitat heterogeneity was positively correlated with PD.ses and taxonomic diversity (c), (e), while geomorphological dynamics did not present any significant correlation with any of the diversity facets (d), (f).

Fig. 6a). In other words, overall, larger islands had higher FD.ses, despite a negative effect of habitat heterogeneity on FD.ses. In addition, we found that geomorphological dynamics did not significantly affect – neither directly nor via area and habitat heterogeneity – any of the diversity facets. The model using historic area (Fig. 6b explained 59, 89 and 79% of the variance for FD.ses, PD.ses and taxonomic diversity. Historic area emerged as the main driver of all diversity facets (standardized effects = 0.77, 0.71 and 0.65 for FD.ses, PD.ses and taxonomic diversity, respectively). However, this model unveiled an indirect effect of geomorphological dynamics on phylogenetic and taxonomic diversity via habitat heterogeneity (standardized effect via habitat heterogeneity = −0.16 for PD.ses and taxonomic diversity). In contrast, no significant relationship between historic area and habitat heterogeneity was found.

Discussion

The West and East Frisian Islands are a comparatively young and highly dynamic island system. They are characterized by

a large range of island sizes and different degrees of habitat diversity. Typical geomorphological dynamics of a barrier island system puts island plant communities under constant disturbances, such as storm surges, tidal floods and erosion and sedimentation caused by wind and water action. Yet, our results revealed that while geomorphological dynamics did play a role shaping multifaceted diversity via influencing habitat heterogeneity, area was the most important driver of all three facets of diversity. Area was also closely related to habitat heterogeneity, showing that they are both relevant and not independent of each other. Most islands showed lower FD.ses and PD.ses than expected by chance (underdispersed) but the few islands larger than 30 km² showed closer to random or higher than expected (overdispersed) patterns for FD.ses. Even though we accounted for differences in species richness, FD.ses and PD.ses showed a strong relationship with area, suggesting that functionally and phylogenetically unique species are accumulating on larger islands. The influence of area
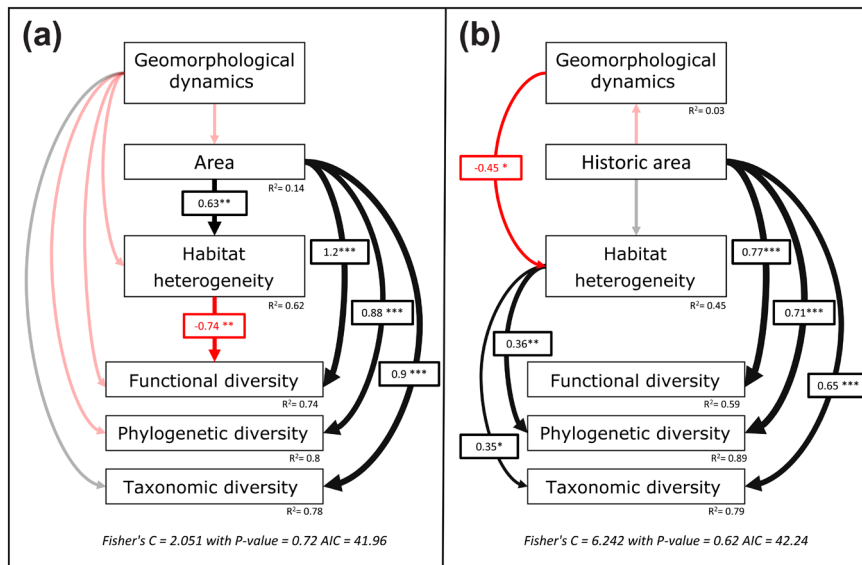
Figure 6. Piecewise structure equation models with black arrows denote positive relationships, and red arrows negative ones. Arrows for non-significant paths (p ≥ 005) are semi-transparent and asterisks represent level of significance: 0 '***', 0.001 '**', and 0.01 '*' 0.05. The thickness of the significant paths has been scaled based on the magnitude of the standardized regression coefficient model. Model (a) quantifies modern island area as the sum of all natural and semi-natural habitats on each island, while model (b) uses historic area from the baseline year 1700 (with the exception of Rottumerplaat island which is from 1900).

via habitat heterogeneity, while weaker, was significant, with an unexpected negative effect on FD.ses.

Functional underdispersion occurred on islands smaller than 30 km^2, while functional diversity increased on larger islands. On the one hand, functional underdispersion is commonly attributed to environmental filtering (Mazel and Thuiller 2020). The Frisian islands are constantly exposed to disturbances caused by wave and wind action, as well as storm surges, which are even more pronounced on smaller islands due their lack of taller dunes and more consolidated sediment. Therefore, the harsh environment of these islands may narrow the range in suitable trait values. On the other hand, competitive exclusion can also lead to underdispersion, depending on the trait being analyzed (Mayfield and Levine 2010, Kraft et al. 2015b). Yet, disentangling abiotic from biotic filtering processes based solely on FD.ses patterns is an intricate task or even impossible (Mazel and Thuiller 2020).

The indication that plants on the Frisian islands are functionally highly similar is further supported by PD.ses, which also shows underdispersion for most of the islands. Given that the description of a functional role might involve an unknown combination of traits, functional diversity has been used as proxy of functional diversity (Prinzing et al. 2001, Cadotte et al. 2009, Cavender-Bares et al. 2009), based on the assumption that phylogenetically closer species are functionally more similar due to phylogenetic trait conservatism.

The shape of FDAR and PDAR curves are in line with previous studies that showed generally underdispersion, which decreases as area increases (Smith et al. 2013, Carvajal-Endara et al. 2017, Zhang et al. 2021). In our study, the difference between the shape of FDAR and SAR curves can be explained by the influence that underlying functional data

have on FDAR. Underdispersed functional diversity causes FDAR curves to depart from SAR curves, instead of mirroring it (Mazel and Thuiller 2020). As FD.ses scales with area, islands larger than 30 km^2 turn from underdispersed to overdispersed or random, which is a pattern that could be influenced by anthropogenic activities. Larger islands with bigger populations are more subject to human modifications (e.g. fixation of dunes, grazing) which interfere with the natural habitats (e.g. dunes and salt marshes). These interferences can artificially create opportunities for new species to come in, which will potentially increase the range of trait values that are represented. Additionally, some species require a minimum area for maintaining viable populations and are filtered out on smaller islands (Zhang et al. 2021). The similarity in the shape of the PDAR and SAR curves can be attributed to the high correlation between PD.ses and taxonomic diversity; this correlation shows that the increase in number of species comes from species of different families (and different traits), reflecting the habitat heterogeneity correlation with PD.ses. This relationship, however, disappears or becomes weaker once we take area (or historic area) into consideration in the SEMs, as PD.ses is greatly influenced by area (or historic area). The influence of area on FD.ses via negative effects of habitat heterogeneity on FD.ses is unexpected and differs from other diversity facets. This unexpected relationship may emerge because, high habitat heterogeneity in a limited space, such as on the islands of Baltrum, Norderney and Langeoog, causes a reduction in the amount of effective area available per habitat, also known as area-heterogeneity trade-off (Allouche et al. 2012). This could lead to 1) stochastic extinctions or 2) increased competition pressure favoring a specific set of traits of stronger competitors, reducing trait variation. The area-heterogeneity

trade-off diminishes as island area grows or habitat heterogeneity declines, like on Texel and Terschelling and Ameland, which will in turn increase FD.ses. However, this effect was no longer present in the SEM using historic area. This can be explained by historic area being not directly correlated with habitat heterogeneity, which in turn diminishes the influence of habitat heterogeneity on FD.ses. The contrast between the two SEMs also highlights how area and habitat heterogeneity are intertwined, which makes it notoriously challenging to disentangle their relative effects on diversity (Hortal et al. 2009).

Despite area being the best predictor of habitat heterogeneity and multifaceted diversity, linear models and the SEM using historic area highlight the underlying role of geomorphological dynamics influencing habitat heterogeneity and subsequently, PD.ses and taxonomic diversity. A higher degree of geomorphological dynamics and repeated disturbances makes it more difficult for some habitats to be formed and maintained. This includes habitats such as high marshes and gray dunes, which provide a less disturbed environment and consequently harbor higher number of species (Leuschner and Ellenberg 2018). One possible explanation for the absence, weak or inconsistent effects of geomorphological dynamics on multifaceted diversity is that in highly dynamic systems, such as barrier islands, geomorphological dynamics affect island plants on smaller time scales. For instance, processes including daily tide changes and seasonal storms may influence island composition, making it hard for the long-term metrics to capture the influence of geomorphology dynamics on plant diversity. Alternatively, one may argue that since the geomorphological dynamics of the islands have a direct impact on the abundance of species on the islands (e.g. by breaking monospecies communities of mature saltmarshes (de Groot et al. 2017), the diversity metrics we used, which are richness based, might been unable to fully capture the variations caused by the long-term geomorphological dynamics of the Frisian islands.

Our results on the influence of islands characteristics (geomorphological dynamics, area and habitat heterogeneity) on taxonomic diversity of plants contrast with those found by Scherber et al. (2018), which in a study on the East Frisian islands found that habitat heterogeneity and geomorphological dynamics were the best predictors to plant taxonomic diversity. This difference might at least partly arise from differences in the underlying data and statistical approach used. For instance, our study considered seven additional islands in the Western part (on top of the ten East Frisian islands) which increased the range of island area size as the West Frisian islands are considerably larger than the East Frisian ones. Furthermore, our study could greatly benefit from data on species abundances, which would make it possible to better assess the impact of the geomorphological dynamics and abundance weighted measure of functional and phylogenetic diversity. Another caveat is the assumption that habitats are independent entities, which most of the cases is not met, since different habitats often share the same species. Therefore, if the proportion of shared species by habitat is not included, habitat heterogeneity may fall short to capture the real heterogeneity.

Finally, our study adds to a growing body of literature on the scale dependency of functional and phylogenetic diversity. Our results also demonstrate that looking at multifaceted diversity can yield relevant information on the drivers and underlying mechanisms of insular plant diversity. Our research also contributes to the general understanding of island dynamics and their temporal scale. Using barrier islands as a study system, we show that for this highly dynamic system, although historical dynamics in island geomorphology influence plant diversity, area is still the strongest driver.

Author contributions

Thalita Ferreira-Arruda: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Nathaly R. Guerrero-Ramírez**: Conceptualization (supporting); Formal analysis (equal); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Pierre Denelle**: Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Patrick Weigelt**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Michael Kleyer**: Data curation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Holger Kreft**: Conceptualization (equal); Data curation (supporting); Funding acquisition (lead); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06238>.

Data availability statement

Data is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.d2547d84p> (Ferreira-Arruda et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Ackerly, D. D. and Donoghue, M. J. 1998. Leaf size, sapling allometry and Corner's rules: phylogeny and correlated evolution in maples (Acer). – Am. Nat. 152: 767–791.

Ali, J. R. 2017. Islands as biological substrates: classification of the biological assemblage components and the physical island types. – J. Biogeogr. 44: 984–994.

Allouche, O. et al. 2012. Area–heterogeneity tradeoff and the diversity of ecological communities. – Proc. Natl Acad. Sci. USA 109: 17495–17500.

Barajas-Barbosa, M. P. et al. 2020. Environmental heterogeneity dynamics drive plant diversity on oceanic islands. – J. Biogeogr. 47: 2248–2260.

Bauer, B. et al. 2021. Functional trait dimensions of trophic metacommunities. – Ecography 44: 1486–1500.

Ben-Hur, E. and Kadmon, R. 2020. Heterogeneity-diversity relationships in sessile organisms: a unified framework. – Ecol. Lett. 23: 193–207.

Blonder, B. 2018. Hypervolume concepts in niche- and trait-based ecology. – Ecography 41: 1441–1455.

Blonder, B. et al. 2014. The n-dimensional hypervolume. – Global Ecol. Biogeogr. 23: 595–609.

Breiman, L. 2001. Random forests. – Mach. Learn. 45: 5–32.

Cadotte, M. W. et al. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. – PLoS One 4: e5695.

Carvajal-Endara, S. et al. 2017. Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. – Ecol. Lett. 20: 495–504.

Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. – Ecol. Lett. 12: 693–715.

Chao, A. et al. 2014. Unifying species diversity, phylogenetic diversity, functional diversity and related similarity and differentiation measures through hill numbers. – Annu. Rev. Ecol. Evol. Syst. 45: 297–324.

Chapin, F. S. 1980. The mineral nutrition of wild plants. – Annu. Rev. Ecol. Syst. 11: 233–260.

Connor, E. F. and McCoy, E. D. 2001. Species–area relationships. – In: Scheiner, S. M. (ed.), Encyclopedia of biodiversity. Elsevier, pp. 397–411.

Davis, R. A. (ed.) 1994. Geology of Holocene Barrier Island Systems. – Springer.

de Bello, F. et al. 2021. Handbook of trait-based ecology. – Cambridge Univ. Press.

de Groot, A.V., Oost, A.P., Veeneklaas, R.M. et al 2017. Tales of island tails: biogeomorphic development and management of barrier islands. – J Coast Conserv 21: 409–419.

Diaz, S. et al. 2004. The plant traits that drive ecosystems: evidence from three continents. – J. Veg. Sci. 15: 295–304.

Díaz, S. et al. 2016. The global spectrum of plant form and function. – Nature 529: 167–171.

Durka, W. and Michalski, S. G. 2012. Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. – Ecology 93: 2297.

Eisma, D. and Wolff, W. J. 1980. The development of the westernmost part of the Wadden Sea in historical time, Rotterdam. – In: Dijkema, K. S. et al. (eds), Geomorphology of the Wadden Sea area. A. A. Balkema, Rotterdam, pp. 95–103.

Ernstsen, V. B. et al. 2006. Quantification of dune dynamics during a tidal cycle in an inlet channel of the Danish Wadden Sea. – Geo-Mar. Lett. 26: 151–163.

Fahrig, L. et al. 1993. Distribution of barrier island plants in relation to overwash disturbance: a test of life history theory. – J. Coastal Res. 9: 403–412.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. – Biol. Conserv. 61: 1–10.

Farquhar, G. et al. 2002. Optimal stomatal control in relation to leaf area and nitrogen content. – Silva Fenn. 36: 625–637.

Ferreira-Arruda, T. et al. 2022. Data from: Island area and historical geomorphological dynamics shape multifaceted diversity of barrier island floras. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.d2547d84p>.

Fitzgerald, D. M. et al. 1984. Control of barrier island shape by inlet sediment bypassing: East Frisian Islands, West Germany. – Mar. Geol. 60: 355–376.

Garnier, É. et al. 2016. Plant functional diversity: organism traits, community structure and ecosystem properties. – Oxford Univ. Press.

Gillespie, R. G. and Roderick, G. K. 2002. Arthropods on islands: colonization, speciation and conservation. – Annu. Rev. Entomol. 47: 595–632.

Gotelli, N. J. and Graves, G. R. 1996. Null models in ecology. – Smithsonian Inst. Press.

Groot, A. V. de et al. 2017. Tales of island tails: biogeomorphic development and management of barrier islands. – J. Coastal Conserv. 21: 409–419.

He, F. and Legendre, P. 2002. Species diversity patterns derived from species–area models. – Ecology 83: 1185–1198.

Heaney, L. R. 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. – Global Ecol. Biogeogr. 9: 59–74.

Homeier, H. et al. 2010. Historisches Kartenmaterial nach Homeier. Berichte der Forschungsstelle Küste. – NLWKN.

Hortal, J. et al. 2009. Island species richness increases with habitat diversity. – Am. Nat. 174: E205–E217.

Isabwe, A. et al. 2019. Community assembly mechanisms underlying the core and random bacterioplankton and microeukaryotes in a river–reservoir system. – Water 11: 1127.

Jarzyna, M. A. and Jetz, W. 2018. Taxonomic and functional diversity change is scale dependent. – Nat. Commun. 9: 2565.

Karadimou, E. K. et al. 2016. Functional diversity exhibits a diverse relationship with area, even a decreasing one. – Sci. Rep. 6: 35420.

Kattge, J. et al. 2020. TRY plant trait database – enhanced coverage and open access. – Global Change Biol. 26: 119–188.

Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology. – Bioinformatics 26: 1463–1464.

Kisel, Y. and Barraclough, T. G. 2010. Speciation has a spatial scale that depends on levels of gene flow. – Am. Nat. 175: 316–334.

Kleyer, M. et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. – J. Ecol. 96: 1266–1274.

Kleyer, M. et al. 2014. Mellum: a highly dynamic landscape, though not for plants. – In: Hellwig, U. and Stock, M. (eds), Dynamic Islands in the Wadden Sea, Trilateral Salt, Marsh and Dunes Expert Group, Common Wadden Sea Secretariat (CWSS), Wilhelmshaven, Germany, pp. 29–43.

Kleyer, M. et al. 2019. Trait correlation network analysis identifies biomass allocation traits and stem specific length as hub traits in herbaceous perennial plants. – J. Ecol. 107: 829–842.

Klotz, S. and Durka, W. 2002. BIOLFLOR–Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in

Deutschland. – Schriftenreihe für Vegetationskunde 38. Bundesamt für Naturschutz.

Kraft, N. J. B. et al. 2015a. Community assembly, coexistence and the environmental filtering metaphor. – Funct. Ecol. 29: 592–599.

Kraft, N. J. B. et al. 2015b. Plant functional traits and the multidimensional nature of species coexistence. – Proc. Natl Acad. Sci. USA 112: 797–802.

Kreft, H. et al. 2008. Global diversity of island floras from a macroecological perspective. – Ecol. Lett. 11: 116–127.

Latham, R. E. et al. 1993. Continental comparisons of temperate-zone tree species diversity. – <www.semanticscholar.org/paper/Continental-comparisons-of-temperate-zone-tree-Latham-Ricklefs/50c8e400bda3ba09bd3dfb85fc0715269b36b548>.

Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution and systematics. – Methods Ecol. Evol. 7: 573–579.

Leibold, M. A. and Chase, J. M. 2018. Metacommunity ecology. – Princeton Univ. Press.

Leuschner, C. and Ellenberg, H. 2018. Ecology of central European non-forest vegetation: coastal to alpine, natural to man-made habitats, 6th edn. – Springer.

Losos, J. B. and Ricklefs, R. E. 2010. The theory of island biogeography revisited. – Princeton Univ. Press.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

Matthews, T. J. et al. 2015. Ecological traits reveal functional nestedness of bird communities in habitat islands: a global survey. – Oikos 124: 817–826.

Matthews, T. J. et al. (eds) 2020. The species–area relationship: theory and application. – Cambridge Univ. Press.

Matthews, T. J. et al. 2019. sars: an R package for fitting, evaluating and comparing species–area relationship models. – Ecography 42: 1446–1455.

Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – Ecol. Lett. 13: 1085–1093.

Mayr, E. 1963. Animal species and evolution. – Harvard Univ. Press.

Mazel, F. and Thuiller, W. 2020. Functional and phylogenetic diversity–area relationships. – In: Matthews, T. J. et al. (eds), The species–area relationship: theory and application. Cambridge Univ. Press, pp. 107–132.

Mazel, F. et al. 2014. Multifaceted diversity-area relationships reveal global hotspots of mammalian species, trait and lineage diversity. – Global Ecol. Biogeogr. 23: 836–847.

Minden, V. and Kleyer, M. 2015. Ecosystem multifunctionality of coastal marshes is determined by key plant traits. – J. Veg. Sci. 26: 651–662.

Minden, V. et al. 2012. Plant trait–environment relationships in salt marshes: deviations from predictions by ecological concepts. – Perspect. Plant Ecol. Evol. Syst. 14: 183–192.

Moles, A. T. et al. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. – J. Ecol. 92: 384–396.

Moles, A. T. et al. 2009. Global patterns in plant height. – J. Ecol. 97: 923–932.

Nationale Databank Flora en Fauna 2015. NDFF distribution atlas. – Floron 2014.

Negoita, L. et al. 2016. Isolation-driven functional assembly of plant communities on islands. – Ecography 39: 1066–1077.

Niedringhaus, R. et al. 2008. Die Flora und Fauna der Ostfriesischen Inseln. – Nationalpark Niedersächsisches Wattenmeer.

Oost, A. P. et al. 2012. Barrier island management: lessons from the past and directions for the future. – Ocean Coastal Manage. 68: 18–38.

Poorter, H. et al. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. – New Phytol. 182: 565–588.

Prinzing, A. et al. 2001. The niche of higher plants: evidence for phylogenetic conservatism. – Proc. R. Soc. B 268: 2383–2389.

QGIS Development Team 2020. QGIS geographic information system. – Open Source Geospatial Foundation.

Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.

Scherber, C. et al. 2018. A barrier island perspective on species-area relationships. – Ecol. Evol. 8: 12879–12889.

Schöpke, B. et al. 2019. Do dispersal traits of wetland plant species explain tolerance against isolation effects in naturally fragmented habitats? – Plant Ecol. 220: 801–815.

Shipley, B. 2016. Cause and correlation in biology, 2nd edn. – Cambridge Univ. Press.

Silverman, B. 1986. Density estimation for statistics and data analysis. – Chapman and Hall.

Smith, A. B. et al. 2013. Characterizing scale-dependent community assembly using the functional–diversity–area relationship. – Ecology 94: 2392–2402.

Stekhoven, D. J. and Bühlmann, P. 2012. MissForest – non-parametric missing value imputation for mixed-type data. – Bioinformatics 28: 112–118.

Streif, H. 1989. Barrier islands, tidal flats and coastal marshes resulting from a relative rise of sea level in East Frisia on the German North Sea coast. – In: van der Linden, W. J. M. et al. (eds), Coastal lowlands: geology and geotechnology. Springer, pp. 213–223.

Swenson, N. G. 2011. The role of evolutionary processes in producing biodiversity patterns and the interrelationships between taxonomic, functional and phylogenetic biodiversity. – Am. J. Bot. 98: 472–480.

Swenson, N. G. 2014. Functional and phylogenetic ecology in R. – Springer.

Tamis, W. et al. 2004. Standaardlijst van de Nederlandse flora 2003. – Gorteria 30: 101–195.

The Plant List 2010. Ver. 1.1. – <www.theplantlist.org/>.

Thompson, K. et al. 1993. Seed size and shape predict persistence in soil. – Funct. Ecol. 7: 236.

Tilman, D. 2013. Functional diversity. – In: Levin, S. A. (ed.), Encyclopedia of biodiversity. Elsevier, pp. 587–596.

Triantis, K. A. et al. 2012. The island species–area relationship: biology and statistics. – J. Biogeogr. 39: 215–231.

Tucker, C. M. et al. 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology. – Biol. Rev. 92: 698–715.

Turner, W. R. et al. 2005. Scale-dependence in species–area relationships. – Ecography 28: 721–730.

Wang, P. and Roberts Briggs, T. M. 2015. Chapter 10 – Storm-induced morphology changes along barrier islands and post-storm recovery. – In: Shroder, J. F. et al. (eds), Coastal and marine hazards, risks and disasters. Elsevier, pp. 271–306.

Wang, X. et al. 2013. Phylogenetic and functional diversity area relationships in two temperate forests. – Ecography 36: 883–893.

Warren, B. H. et al. 2015. Islands as model systems in ecology and evolution: prospects fifty years after MacArthur–Wilson. – Ecol. Lett. 18: 200–217.

Webb, C. O. et al. 2002. Phylogenies and community ecology. – Annu. Rev. Ecol. Syst. 33: 475–505.

Weigelt, P. et al. 2016. Late quaternary climate change shapes island biodiversity. – Nature 532: 99–102.

Weigelt, P. et al. 2020. GIFT – a Global Inventory of Floras and Traits for macroecology and biogeography. – J. Biogeogr. 47: 16–43.

Weiss, M. and Banko, G. 2018. Ecosystem Type Map v3.1-terrestrial and marine ecosystems. – ETC/BD report to the EEA.

Whittaker, R. J. et al. 2008. A general dynamic theory of oceanic island biogeography. – J. Biogeogr. 35: 977–994.

Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – Nature 428: 821–827.

Wyse, S. V. and Hulme, P. E. 2021. Limited evidence for a consistent seed mass-dispersal trade-off in wind-dispersed pines. – J. Ecol. 109: 284–293.

Zhang, A. et al. 2021. Nonlinear thresholds in the effects of island area on functional diversity in woody plant communities. – J. Ecol. 109: 2177–2189.