




Plant dispersal characteristics shape the relationship of diversity with area and isolation

Anna Walentowitz^{1,2}  | Claudia Troiano^{3,4}  | Julie B. Christiansen^{3,5}  |
Manuel J. Steinbauer^{2,3,6}  | Anders S. Barfod³ 

¹Chair of Biogeography, University of Bayreuth, Bayreuth, Germany

²Bayreuth Center of Ecology and Environmental Research (BayCEER) & Bayreuth Center of Sport Science (BaySpo), University of Bayreuth, Bayreuth, Germany

³Department of Biology, Aarhus University, Aarhus C, Denmark

⁴Department of Humanities, University of Naples Federico II, Naples, Italy

⁵Department for Technology and Environment, Vordingborg City, Langebæk, Denmark

⁶Department of Biological Sciences, University of Bergen, Bergen, Norway

Correspondence

Anna Walentowitz, Chair of Biogeography, University of Bayreuth, Bayreuth, Germany.
Email: anna.walentowitz@uni-bayreuth.de

Abstract

Aim: The relation of plant dispersal syndromes with insular species richness patterns remains one of the challenges in island biogeography, especially as people have affected species distribution patterns. This study disentangles how dispersal syndromes influence the relationship of richness with area and isolation while also accounting for the human impact on island biodiversity. It builds on the potential of islands at the mesoscale and of similar origin to contribute to the ongoing discussion in island biogeography on what determines species richness and filtering.

Location: Denmark, 54 islands in the North and Baltic Sea.

Taxon: Vascular plants, including pteridophytes.

Methods: Generalized linear models (GLMs) and linear regressions are used to analyse how dispersal syndromes influence the relationships of species numbers with island area and isolation, as well as island inhabitation and human density, respectively.

Results: Species numbers, seed mass and the proportion of zoochore and anemochore species are positively related to island area while the share of water-dispersed species decreases with increasing area. Isolation is weakly related to mean seed mass but has no explaining power for species numbers and the presence of specific dispersal syndrome on the target islands. Species richness and seed mass were positively related to human presence.

Main conclusions: Human impact for centuries has not overwritten the strong relationship of species richness with area on the Danish Islands but is affecting the shape of this relationship. Island area constitutes a strong filter for different dispersal syndromes and leads to the assumption that heavier and animal-dispersed seeds are positively related to area due to the presence of more bird and mammal species. Human-induced loss of isolation caused by ongoing traffic and the connection of landmasses by bridges and ferries may be a reason for the overall low explanatory power of island isolation.

Handling editor: Alain Vanderpoorten

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2022 The Authors. *Journal of Biogeography* published by John Wiley & Sons Ltd.

KEYWORDS

dispersal pathways, dispersal syndromes, establishment, insular biodiversity, plant species richness, SAR

1 | INTRODUCTION

The forgotten roots of island biogeographic theory can be found in the seminal work of Alvar Palmgren in the Finnish Åland archipelago. Already 50 years before MacArthur and Wilson (1967), he developed ideas similar to the equilibrium theory of island biogeography and suggested that isolation from the mainland and area balance species richness on islands (Palmgren, 1915–1917; Palmgren, 1921; Palmgren, 1927). Palmgren's (1915–1917) work on plants in the Åland archipelago inspired the Swedish scientist Olof Arrhenius to formulate the first mathematical expression of the species-area relationship (henceforth SAR) (Arrhenius, 1921), which remains one of the most essential models explaining species richness in various island systems around the world (Triantis et al., 2012). Palmgren additionally argued that the dispersal and establishment of particular species, being dependent on chance and priority effects, govern species compositions on islands (Palmgren, 1915–1917; Palmgren, 1921; von Numers & van der Maarel, 1998). This early vision initiated an intellectual debate between Palmgren on the one side and his contemporaries Paul Jaccard and Ole Eklund on the other side (Swenson, 2019; von Numers & van der Maarel, 1998). Both Jaccard and Eklund opposed Palmgren's idea of area and isolation effects suggesting habitat availability and quality (and hence competitive exclusion) as the main drivers of species richness on islands (Eklund, 1931; Eklund, 1937; Jaccard, 1922; Järvinen, 1982; Palmgren, 1915–1917; Palmgren, 1921; Palmgren, 1925; Palmgren, 1927).

The disagreement between Palmgren, Eklund and Jaccard is symptomatic for the field of island biogeography and it has embossed the discussions on what determines insular species richness ever since (Proença & Pereira, 2013; Scherber et al., 2018; Triantis et al., 2003; Triantis et al., 2005). Several studies indicate that island area is the strongest predictor for species richness in different island systems around the world, followed by isolation (Abbott, 1974; Chown et al., 1998; Kreft et al., 2008; Lomolino, 1982). However, a number of confounding factors such as habitat diversity, island age and disturbance history have been suggested to drive species richness on islands as well (Heaney, 2000; Losos & Ricklefs, 2010; Losos & Schluter, 2000; Matthews et al., 2019; Rosenzweig, 1995; Scherber et al., 2018; Triantis et al., 2012; Whittaker et al., 2008). Thereby, the different mechanisms are not mutually exclusive and may operate either individually or in combination (Connor & McCoy, 1979; Kohn & Walsh, 1994; Ricklefs & Lovette, 1999; Rosenzweig, 1995; Triantis et al., 2003). For special island systems such as barrier islands or tiny islands, habitat diversity may have a stronger influence on species diversity than other drivers (Scherber et al., 2018; Triantis et al., 2006). Furthermore, spatial autocorrelation, latitudinal differences that translate into climatic dissimilarity (Drakare et al., 2006) and the small island effect (Burns et al., 2009;

Dengler, 2010) often make generalizations on diversity patterns on islands difficult. Human alterations of islands add another layer of complexity to species assemblages on islands (Nogué et al., 2021). Revisiting Palmgren's works is a tribute to his pioneering research and frames ongoing discussions on island biogeography.

Alvar Palmgren was aware that species growing in the Åland archipelago were a filtered subsample from a larger species pool found on mainland Scandinavia (Palmgren, 1915–1917). He acknowledged that species filtering by island isolation is dependent on species-specific dispersal traits. Several decades later, seminal work by Carlquist (1966) from the Pacific further demonstrated how species composition depends on prevailing dispersal vectors and how this potentially influences evolutionary dynamics on large oceanic islands. However, despite these early indications, the role of species-specific traits involved in island colonization (i.e. dispersal vectors) and their relation to island characteristics have remained unclear. Few studies have continued this idea and applied it to island systems. Among these, Burns (2005) evaluated dispersal constraints of woody plants on Vancouver Island as a function of fruit characteristics. Another study by Heleno and Vargas (2015) that focuses on long-distance dispersal syndromes suggests sea dispersal and endozoochory as possible important traits for long-distant island colonization. Beyond the importance of zoochory as a dispersal syndrome to overcome long distances it can also result in wider distributions of species within archipelagos (Arjona et al., 2018). Substantial differences in slope and intercept of SARs among the main lineages of land plants have been linked to diaspore size, and hence, their potential for long-distance dispersal by wind (Patiño et al., 2014). Recently, Schrader et al. (2021) used functional diversity in general, including dispersal characteristics, to show that assembly processes of tree species on islands are not random and scale with area.

In this study, we return to Scandinavia to investigate SARs, species' relationships with isolation and human impact, based on dispersal traits and species compositions of plants on 54 Danish islands scattered throughout the Baltic and the North Sea including bays and fjords. We acknowledge the great potential of these islands to investigate patterns of species richness and filtering on islands of similar origin at the mesoscale. Human alterations of the islands add another layer of filtering to the analysis that we account for by taking island inhabitation and human density into the equation. The Danish islands are located in the nemoral zone of northern Europe. They constitute a geographically contrasting study site to current island biogeographic research that mostly takes place on larger archipelagos at subtropical latitudes, often of volcanic origin and with considerable evolutionary dynamics (Borregaard et al., 2015; Jöks & Pärtel, 2019; Valente et al., 2017; in geographical contrast to Korvenpää et al., 2003; MacArthur & Wilson, 1967; McMaster, 2005; Morrison, 2010; Scherber et al., 2018). As demonstrated by the



influential work of Simberloff and Wilson (1969) in the Florida Keys, these smaller, less isolated barrier island systems are governed by unexplored dynamics that remain to be unveiled.

First, we investigate the relative effect of island area, isolation and human impact on plant species richness in 54 Danish saltwater and brackish water islands. After controlling for area, we expect more distant islands to have a lower species richness, with distance from the mainland being the second most important driver beside area (according to MacArthur & Wilson, 1967). Human impact is expected to increase species richness due to the introduction of agricultural and ornamental plants.

In a second step, we disentangle the driving mechanisms by analysing the potential presence of constraining dispersal filters acting on the regional species pool. Given the strong effect of island area on plant species richness (Kreft & Jetz, 2007), we suspect that island area might act as a dispersal filter (e.g. target-area effect, Lomolino, 1990). After characterizing species by traits associated with dispersal potential (seed mass as well as dispersal strategies; Heleno & Vargas, 2015), we expect (1) a positive relationship between seed mass and island area, since endozoic and epizoic plant species have heavier seeds and the overall number of mammals and birds that are typically involved in this kind of dispersal will increase as a function of island size. This translates into the expectation of (2) an increase in the percentage of zoochore species with increasing area but (3) a decrease in the percentage of hydrochore species because of the relationship between coastline and area (when coastline doubles, area roughly quadruples). Furthermore, we expect (4) the mean seed mass to decrease with increasing isolation, as it would be more likely for smaller seeds to be carried to islands that are further away; (5) the proportion of autochore species to decrease with increasing isolation, as it would be more difficult for sessile species to disperse to great distances without further adaptations.

2 | MATERIALS AND METHODS

2.1 | Study area

We analyse plant species compositions from 54 major Danish islands scattered around the Danish North Sea and Baltic Sea coasts (Figure 1). These islands provide optimal conditions to test for environmental filters as they are all separated from the mainland since the last glaciation 10,000 years ago and have been gradually colonized since then (Böse et al., 2012; Mortensen et al., 2011). Salinity and tidal range influence the islands' vegetation and differ along a gradient from the North to the Baltic Sea (Moeslund et al., 2011). The islands are heavily impacted by human activity, and species assemblages are influenced by agricultural uses and human settlements (Hannus & von Numers, 2010). Acknowledging the islands' anthropogenic alteration is necessary, as a strict distinction between natural and anthropogenic impacts on island flora is impossible on the islands investigated. To account for human alterations we identified inhabited ($n = 18$) and uninhabited islands ($n = 36$) and calculated

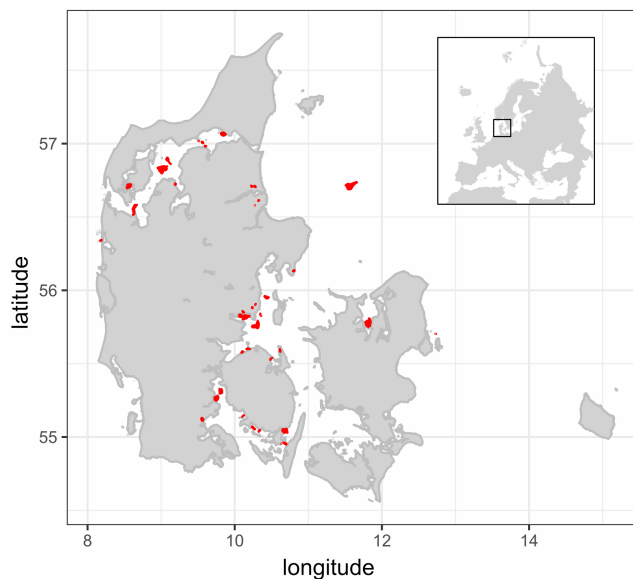


FIGURE 1 The investigated 54 small islands (red) are scattered along the coast of Denmark (location within Europe is indicated in the upper right overview). The map is based on a geographic coordinate system (EPSG 4326, WGS 84).

human density (number of island inhabitants per ha). The number of island inhabitants was compiled from Danmarks Statistik (2021) and for smaller islands, we used Google Earth images (© Google Earth 2021) to verify that no houses were present on the island (human density = 0) (Table S1).

The development of the Danish landscape during the Holocene was determined by an interaction between eustatic sea rise and uplifting of several mm per year. This led to significant changes in the number, size, and positions of islands over a short evolutionary time (von Numers & van der Maarel, 1998). The definition of an island in a shallow sea influenced by sedimentation dynamics and tidal water is far from trivial. Based on recent GIS maps and historical maps, we identified islands as bodies of permanent dryland clearly separated by water in the recent past (last 130 years). Some of the surveys by Wessberg et al. (2011) comprise a cluster of islands with several species lists. The number of islands in these clusters varies from two (e.g. Kyholm) to 23 (Treskelbakkeholm), but the smallest islets were not surveyed.

2.2 | Plant species occurrence data

This study is built on a comprehensive data set compiled by Erik Wessberg and co-workers since 1979. It became available in 2011 on the homepage of the Danish Botanical Society as a series of commented species lists, one for each of the islands or cluster of islands surveyed in total (Wessberg et al., 2011). The complete data set is appropriate for inter-island comparisons at the mesoscale since the surveys were conducted by the same group of botanists. Most of the species on the list were recorded by the authors themselves during field surveys, but they also included species recorded in literature.

We removed literature records before 1950 since this year marks the beginning of the mechanization of Danish agriculture, which has profoundly impacted Danish nature. We used presence-absence data throughout because the abundances recorded in the original data were not complete for all species. It should be noted that we also include naturalized domesticated plants in the analyses, which brings the total number of taxa to 1360 (Table S1). To make the species list comparable across islands, we decided to exclude all taxonomic categories below species level and to merge agamospecies (resulting in 1201 species). The taxonomy follows the authority list for Danish species available online at www.allearter.dk.

2.3 | Species trait data

We gathered trait information on seed mass (mg) as well as dispersal syndromes (zoochory, hydrochory, anemochory, and autochory) for the 1201 species found on the islands from databases. Sources were the Royal Botanic Gardens Kew (2016) and the LEDA database (Kleyer et al., 2008) that provided data for more than one thousand species. For the remaining species, we extracted data from the Ecological Flora of The British Isles (Fitter & Peat, 1994), BIOLFLOR (Klotz et al., 2002), BROTT trait database for plant species of the Mediterranean Basin (Paula et al., 2009), and D³, The Dispersal and Diaspore Database (Hintze et al., 2013). Gaps in the data (roughly 100 species) were filled, when possible, by interpolation based on the traits of other species of the same genus, and ferns and clubmosses were assigned the smallest seed mass value in the dataset.

The data gathered was used to characterize seed mass and dispersal syndromes of each of the islands' species communities. Island community seed mass was quantified as the mean seed mass of all present species. The importance of different dispersal syndromes for reaching and establishing on the island was weighted by the relative percentage of species per island associated with each dispersal type (e.g. species A: 50% zoochory and 50% autochory).

2.4 | Analysis

The species lists of Wessberg et al. (2011) were entered manually into an Excel spreadsheet and the exact geographic position and precise boundaries were determined in GIS. This allowed us to calculate isolation (mean of 2732 m +6508) as the shortest distance to the nearest mainland (species pool; considering the largest islands Saelland, Vendsyssel-Thy and Fyn to be part of continental Denmark), and surface area (mean of 252 ha +502) of the individual islands.

To test the relationship of insular species richness with area, isolation and human presence, using island inhabitation (GLM^{inhab}) or human density (GLM^{pop.dens}) as proxies, we performed GLMs (Poisson family error, log link). We tested for correlation between the continuous variables area, isolation and human density (Pearson's product-moment correlation was <0.2), which can be neglected in

this instance, and log₁₀-transformed the values of all island characteristics (adding 10⁻⁶ for values of zero). Independence of the categorical variable island inhabitation with area and isolation was tested with a Student's *t*-test, which revealed a significant relationship between the variables ($p < 0.001$). We therefore performed two GLMs to explain species numbers of which the GLM^{inhab} includes island inhabitation as an explanatory variable, and GLM^{pop.dens} is based on a subset of only inhabited islands, incorporating population density as an independent variable to account for human alteration of island flora. We used backwards variable selection for model building and the Akaike Information Criterion (AIC) to evaluate model fit. The fitted models were validated by plotting residuals against fitted values. The analysis was repeated with a subset of the data incorporating only spermatophytes and no pteridophytes (ferns, clubmosses and horsetails) to distinguish if the observed patterns are being driven by spores of pteridophytes or seeds of spermatophytes. As the most frequently used function to investigate SAR is the power function (Arrhenius, 1921; Triantis et al., 2012), we fitted its linear version on the log-transformed species numbers and island area to make our results comparable to other findings using the package 'vegan' (Oksanen et al., 2019).

In an additional subsequent regression analysis, we decomposed species richness by dispersal syndromes (zoochory, hydrochory, autochory and anemochory) to examine their relationship with island area after log₁₀-transforming all explanatory variables (adding 10⁻⁶ for values of zero). 95% confidence intervals were calculated. To investigate the presence of area-, isolation- and human-related dispersal constraints, we tested the relationship between mean seed mass per island and the percentage of zoochore, hydrochore, anemochore and autochore species with area and isolation (on all study islands, $n = 54$) and population density (only on inhabited islands, $n = 18$), respectively, using GLMs (Poisson family error, log link). Isolation-related analyses were repeated using a subset of only spermatophytes, excluding pteridophytes. Significance levels are reported as: [*] $0.05 > p > 0.01$; [**] $0.01 > p > 0.001$; [***] $p < 0.001$ throughout the analysis. Pseudo R^2 (Nagelkerke, 1991) was calculated with the package *rms* (Harrell Jr, 2020). All analyses were performed in R (version 4.0.2; R Core Team, 2020) using the packages *tidyverse* (Wickham et al., 2019), *gridExtra* (Aguie, 2017), *jtools* (Long, 2020) and *ggeffects* (Lüdecke, 2018).

3 | RESULTS

Analyses confirm a significant and strong species-area relationship for the 54 Danish islands, a significant but less strong relationship with island inhabitation and human density on inhabited islands, but no relationship between isolation and species richness (Table S2 and S3). Human impact shapes the relationship of the global SAR as inhabited islands (model estimates: area = 0.7***, inhabitation = 0.5***) and islands with a higher population density (model estimates: area = 0.6***, inhabitation = 0.1***) show an overall higher species richness compared to uninhabited islands and less densely



populated islands (Figure 2). Focusing only on spermatophytes and excluding pteridophytes revealed the same pattern (Table S3). Using the power function, the SAR has a regression slope (z) of 0.34.

When comparing species by dispersal syndromes, the strong relationship between species richness and island area remained, with slight differences in intercepts and slopes (Figure 3). The steepest slope was calculated for anemochore species followed by autochore, zoochore and then hydrochore species ($0.43 > 0.42 > 0.41 > 0.34$), with overlapping confidence intervals but differing intercepts of zoochore and hydrochore species (intercept = 1.07 and 1.16, respectively) and of autochore and anemochore species (intercept = 0.66 and 0.59, respectively).

Mean seed mass of plant communities as well as the percentage of species with zoochore, hydrochore and anemochore dispersal syndromes were all significantly related with island area with the exception of autochore species (Figure 4a–e; Table S4). In detail, mean community seed mass was significantly increasing with island area (pseudo $R^2 = 0.46^{***}$). There was a positive relationship between the proportion of zoochore species (pseudo $R^2 = 0.29^*$) and anemochore

(pseudo $R^2 = 0.29^*$) species with island area, while the percentage of hydrochore species declines with increasing island area (pseudo $R^2 = 0.53^{***}$).

Community seed mass was also found to be dependent on isolation but was less strongly associated with isolation compared to island area (pseudo $R^2 = 0.03^{**}$, Figure 4f). No significant relationships between the percentage of zoochory, hydrochory, anemochory and autochory with isolation were detected ($p > 0.05$, Figure 4g–j). Human density of inhabited islands as a proxy for human impact was not related to any of the dispersal syndromes.

4 | DISCUSSION

Despite the strong human impact for centuries on the 54 Danish islands surveyed by Wessberg et al. (2011) and targeted in this study, we recovered a strong relationship of species per island with area, confirming the global SAR pattern (Triantis et al., 2012). The slope of the regression line representing this relationship was 0.34, which lies

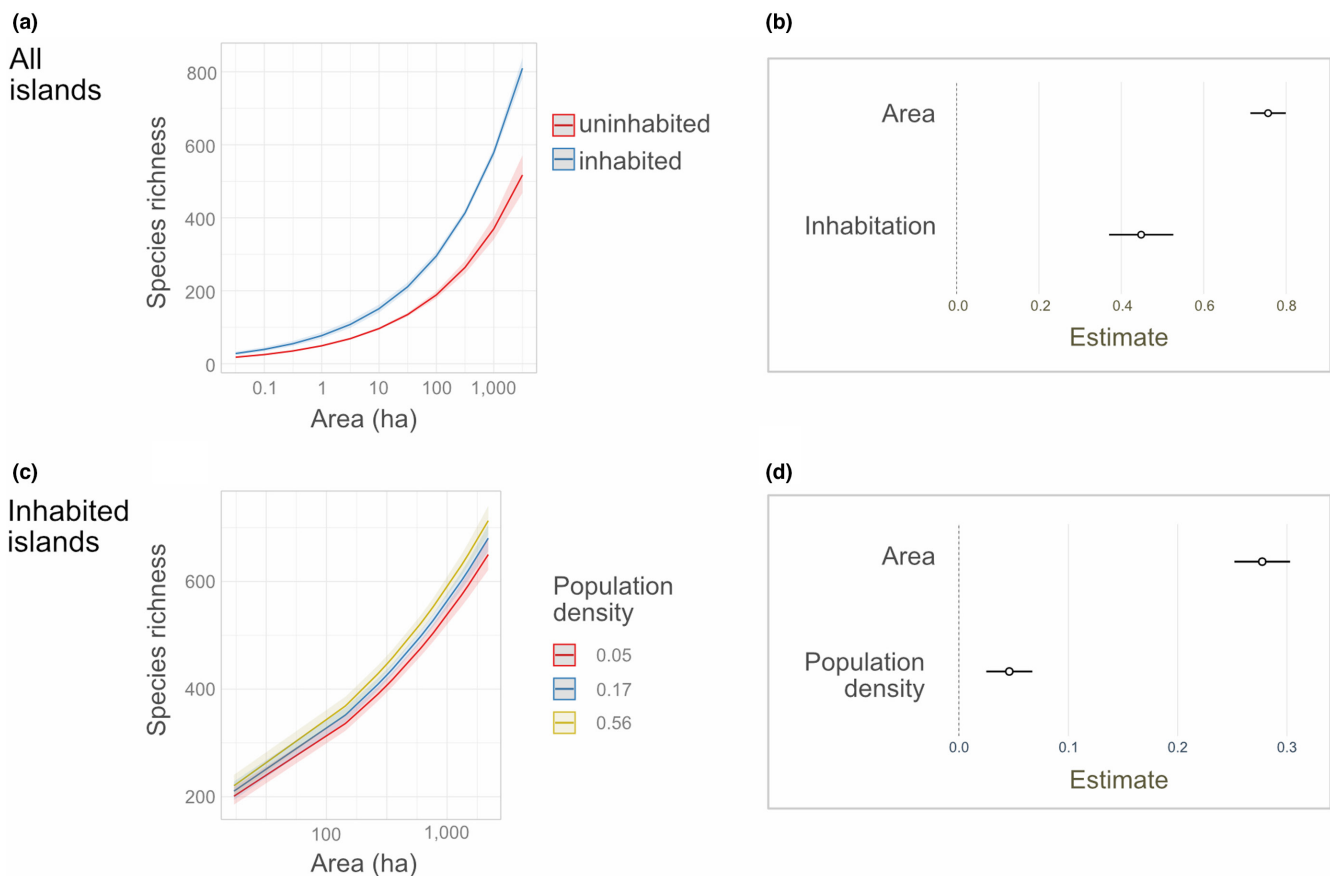


FIGURE 2 Relationship of plant species richness with island area and island inhabitation on all study islands (GLM^{inhab}; $n = 54$; top) as well as the relationship of plant species richness with area and population density (inhabitants per ha) on inhabited islands (GLM^{pop_dens}; $n = 18$; bottom) based on GLMs. Mean model predictions of the number of species considering area and (a) island inhabitation or (c) population density as explanatory variables are displayed. 95% confidence intervals are given as shaded areas. The x-axes (area) and the legend (population density) respond to linear scale. Regression coefficient plots show the relationship of area and island inhabitation (b) or population density (d) with species numbers.

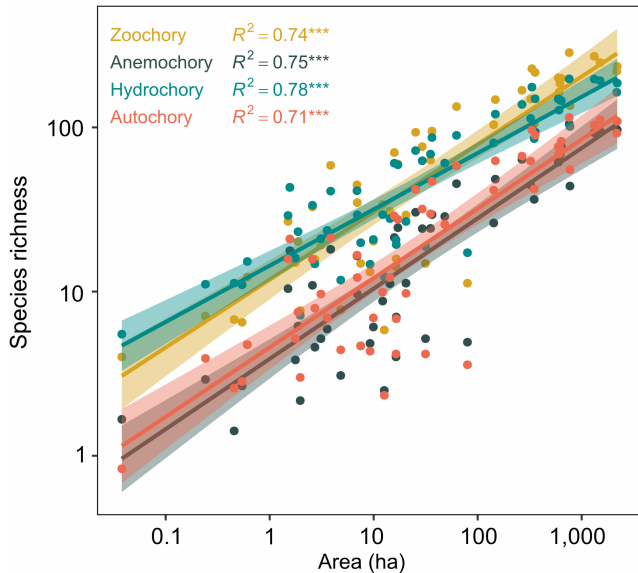


FIGURE 3 Relationship between species richness and island area ($n = 54$ Danish islands) among plant groups characterized by different dispersal syndromes in log–log space. Zoochore ($R^2 = 0.74^{***}$, $z = 0.41$) and hydrochore ($R^2 = 0.78^{***}$, $z = 0.34$) species exhibit higher intercept values than anemochore ($R^2 = 0.75^{***}$, $z = 0.43$) and autochore ($R^2 = 0.71^{***}$, $z = 0.42$) species, while slopes differ only slightly. 95% confidence interval are given as shaded areas. The axes respond to linear scale.

within the common range (Triantis et al., 2012). Comparing the SARs per dispersal syndrome revealed only slight differences in slope, that might be attributed to the high variability of this relationship in general (Sólymos & Lele, 2012) or can be the result of unknown relationships between area and dispersal-related plant characteristics. In addition, SAR intercepts of plant species with hydrochore and zoochore dispersal syndromes were higher compared to anemochore and autochore species, which translates into a higher richness of water- and animal-dispersed species on islands compared to wind- and self-dispersed plant species. The difference in intercept between SARs of plants with specific dispersal syndromes most likely reflects their overall representation in the source pool and is not an effect of island characteristics or filtering. Although the dataset contained several islets (39% of all islands were smaller than 10 ha), no patterns hinting at the small island effect (Lomolino & Weiser, 2001) could be detected. Human density as a proxy for anthropogenic impact proved to partly explain richness patterns on the Danish Islands, suggesting that the human dimension should be included as an explanatory variable in such analysis. The intentional and accidental introduction of alien plant species and the creation of additional habitats (e.g. agricultural fields, meadows and gardens) can explain higher species numbers under increased human impact. However, this relationship should be interpreted carefully, as human density is likely to scale with area and small islands are commonly not inhabited. Isolation was not associated with species numbers per island, which contradicts former studies that considered it to be the second most important variable explaining the species numbers on islands

(Kreft & Jetz, 2007; McMaster, 2005) considering only natural drivers of species richness. One explanation is that the targeted island systems are simply not very isolated, exhibiting a mean distance to the mainland of 2700 m and a maximum distance of 44,000 m, and lever out the impact of isolation on richness patterns. Additionally, the low explaining power of isolation may be attributed to the loss of floristic distances as humans function as vectors due to ongoing traffic and the connection of landmasses by bridges and ferries. Although the distance to the mainland remains the same, the biogeographic distance and dispersal barrier for species become smaller. Additionally, most studies investigating isolation as a predictor for species richness were limited to vascular plants (Diver, 2008; Kreft et al., 2008; Weigelt & Kreft 2012; Weigelt et al., 2015), whereas our dataset also included ferns, clubmosses and horsetails, which might be less affected by isolation as they are characterized by extremely light diaspores (Kreft et al., 2010). However, repeated analysis based only on spermatophytes showed that isolation does not explain species numbers on the targeted islands. Subsequently, pteridophytes, which represent less than 3% of all study species, do not govern richness patterns. Since isolation is weakly related to seed mass and not at all with any dispersal syndrome, all species in the species pool seem to be able to reach the islands of the study regardless of their distance to mainland, which then could lead to the observed species richness patterns. We thus have to reject our expectation that the proportion of autochore species irrevocably decreases with augmenting isolation from the mainland for the target islands.

The general tendency of island area as a significant explaining variable of species richness is also reflected in its importance for the occurrence of dispersal syndromes per island and for community seed mass. The analysis confirms the expected positive relationship between seed mass and the percentage of zoochore species with island area. Both observations might have a common explanation, and we suggest this to be a consequence of larger islands attracting more mammal and bird species supporting plant dispersal, also of heavier seeds. In accordance, Liu et al. (2019) use seed size of woody plants as a proxy for seed weight and revealed a negative trend with the island area. The explanation of the authors is that for smaller islands, birds gain more importance for dispersal compared to mammals, with birds being a vector for smaller seeds while mammals can disperse larger seeds (Liu et al., 2019). Fragmentation experiments reveal that smaller patches sustain fewer mammals (Hagen et al., 2012; Heinen et al., 2018), which can serve to explain our observations, if islands scattered along the coast of large mainland areas are considered to be a fragmented landscape. The importance of zoochory for dispersal has also been reported by Burns (2005) for woody angiosperms on Vancouver Island and Heleno and Vargas (2015) for long-distance dispersal of angiosperm species.

On islands, the occurrence of especially large seeds is a known phenomenon, which is the result of evolutionary processes (Kavanagh & Burns, 2014). The Danish islands are in this regard not comparable to true oceanic islands that have undergone a long history of isolated evolution that results in the occurrence of high percentages of endemic plants. The flora of the Danish islands does

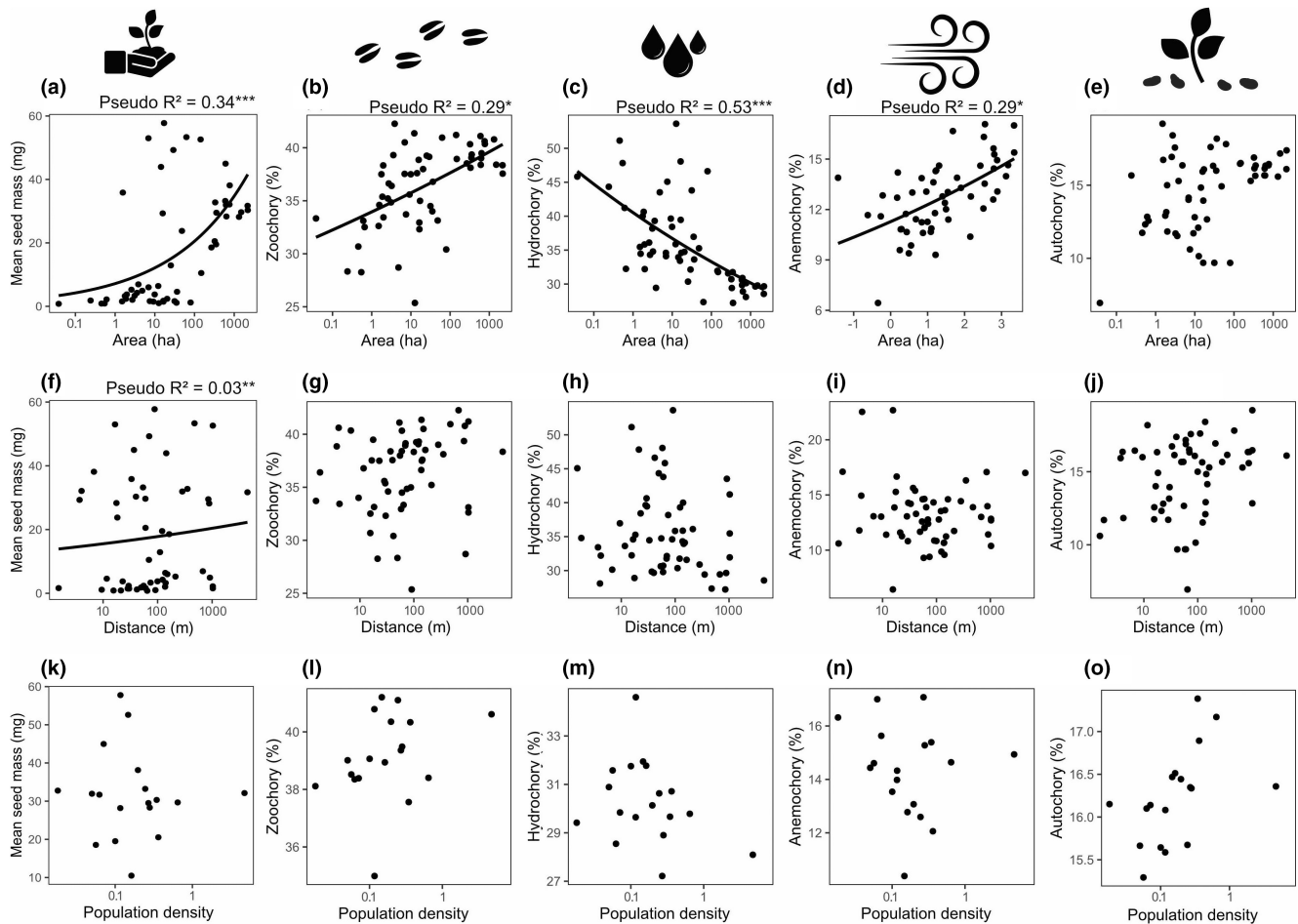


FIGURE 4 The upper row shows the relationship of area with (a) seed mass (pseudo $R^2 = 0.34^{***}$), (b) the percentage of animal (pseudo $R^2 = 0.29^*$), (c) water (pseudo $R^2 = 0.53^{***}$), (d) wind (pseudo $R^2 = 0.29^*$) and (e) self-dispersed ($p > 0.05$) plant species. In the centre row, the relationship of isolation (f) with seed mass (pseudo $R^2 = 0.03^{**}$) and the non-significant relationships with isolation and the percentages of (g) animal, (h) water and (i) wind, and (j) self-dispersed species are displayed. Below, human density of inhabited islands is not related to (k) seed mass or (l-o) any of the dispersal syndromes ($p > 0.05$). The models related to area and isolation are based on all target islands ($n = 54$) whereas models related to population density were based only on inhabited islands ($n = 18$). Black lines and asterisks indicate significant linear relationships (GLMs; $\alpha = 0.05$) and according pseudo R^2 -values are given.

not differ largely from the species occurring on the nearby mainland (Wessberg et al., 2011). Therefore, our study setup aligns with the groundbreaking work of Simberloff and Wilson (1969) on island biogeography who conducted their experiments in the Florida Keys, which are also located close to the North American continent and thus have no long history of evolution separated from the mainland.

In contrast to the positive relationships between species richness, seed mass, the percentage of zoochore species, and area, a decrease in the percentage of hydrochore species was observed, confirming our expectation based on the fact that coastline doubles while area quadruples. Thus, an increase in island area does not result in the same increase of coastline that commonly is the habitat of hydrochore species. Unexpected is the steep relationship between the number of hydrochore species and area, considering that the number of species that are exclusively hydrochore is very low (<20%). This apparent dichotomy could be due to the relative proportions of other dispersal

vectors increasing more rapidly in relation to area. However, a possible explanation could be that species not exclusively associated with hydrochory reach the island via water transport but, once on the island, their dispersal is more related to other dispersal syndromes.

Despite the large impact of humans on the investigated Danish islands, we found that area was the overriding driver of species richness patterns and also had the greatest filtering effect on plants with differing dispersal syndromes. The human impact variable increased the explanatory power when added to the models predicting insular species richness.

Expanding the set of islands commonly used in island biogeography, as has been done in this study, is needed to challenge theories of island biogeography. Although the Danish islands have undergone anthropogenic alterations, it is astonishing that the general pattern of increasing species numbers with area is strongly visible, confirming the global SAR. Decomposing this relationship by dispersal syndromes enhances the understanding of insular species patterns and filtering, and

taking anthropogenic variables into the equation complements the set of variables explaining species assemblages in these modern times.

ACKNOWLEDGEMENTS

We acknowledge the group of botanists spearheaded by Erik Wessberg, who collected the data set underlying this paper. AW thanks her colleagues from the Sport Ecology working group and the Chair of Biogeography at the University of Bayreuth for their valuable comments on the manuscript and Jan Walentowitz for the graphical support. No permits were needed to work on this project. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R script are fully available on Dryad under the following link: <https://doi.org/10.5061/dryad.r2280gbg0>.

ORCID

Anna Walentowitz  <https://orcid.org/0000-0001-9720-9078>

Claudia Troiano  <https://orcid.org/0000-0003-2448-2721>

Manuel J. Steinbauer  <https://orcid.org/0000-0002-7142-9272>

Anders S. Barfod  <https://orcid.org/0000-0002-6298-1823>

REFERENCES

- Abbott, I. (1974). Numbers of plant, insect and land bird species on nineteen remote islands in the southern hemisphere. *Biological Journal of the Linnean Society*, 6, 143–152.
- Arjona, Y., Nogales, M., Heleno, R., & Vargas, P. (2018). Long-distance dispersal syndromes matter: Diaspore-trait effect on shaping plant distribution across the Canary Islands. *Ecography*, 41, 805–814.
- Arrhenius, O. (1921). Species and area. *Journal of Ecology*, 9, 95–99.
- Auguie, B. (2017). *gridExtra: Miscellaneous functions for "grid" graphics. R package version 2.3*
- Borregaard, M. K., Matthews, T. J., & Whittaker, R. J. (2015). The general dynamic model: Towards a unified theory of Island biogeography? *Global Ecology and Biogeography*, 25, 805–816.
- Böse, M., Lüthgens, C., Lee, J. R., & Rose, J. (2012). Quaternary glaciations of northern Europe. *Quaternary Science Reviews, Quaternary Glaciation History of Northern Europe*, 44, 1–25.
- Burns, K. C. (2005). A multi-scale test for dispersal filters in an Island plant community. *Ecography*, 28, 552–560.
- Burns, K. C., McHardy, P. R., & Shirley, R. P. (2009). The small-Island effect: Fact or artefact? *Ecography*, 32, 269–276.
- Carlquist, S. (1966). The biota of Long-distance dispersal. II. Loss of dispersibility in pacific compositae. *Evolution*, 20, 30–48.
- Chown, S. L., Gremmen, N. J. M., & Gaston, K. J. (1998). Ecological biogeography of Southern Ocean islands: Species area relationships, human impacts, and conservation. *The American Naturalist*, 152, 562–575.
- Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, 113, 791–833.
- Danmarks Statistik (2021). Retrieved from October 25, 2021, www.statbank.dk/BEF4
- Dengler, J. (2010). Robust methods for detecting a small Island effect. *Diversity and Distributions*, 16, 256–266.
- Diver, K. C. (2008). Not as the crow flies: Assessing effective isolation for Island biogeographical analysis. *Journal of Biogeography*, 35, 1040.
- Drakare, S., Lennon, J. L., & Hillebrand, H. (2006). The imprint of the geographical evolutionary and ecological context on species-area relationships. *Ecology Letters*, 9, 215–227.
- Eklund, O. (1931). Über die Ursachen der regionalen Verteilung der Schärenflora Südwest-Finnlands. Eine Kausalitätsanalyse mit besonderer Berücksichtigung der Pflanzenwelt in den Kirchspielen Korpo und Houtskär. *Acta Botanica Fennica*, 8, 1–133.
- Eklund, O. (1937). Klimabedingte Artenareale. *Acta Societatis pro Fauna et Flora Fennica*, 60, 309–326.
- Fitter, A. H., & Peat, H. J. (1994). The ecological Flora database. *Journal of Ecology*, 82, 415–425.
- Hagen, M., Kissling, W. D., Rasmussen, C., De Aguiar, M. A. M., Brown, L. E., Carstensen, D. W., Alves-Dos-Santos, I., Dupont, Y. L., Edwards, F. K., Genini, J., & Guimaraes, P. R., Jr. (2012). 2 - biodiversity, species interactions and ecological networks in a fragmented world. In U. Jacob & G. Woodward (Eds.), *Advances in ecological research, global change in multispecies systems part 1* (pp. 89–210). Academic Press.
- Hannus, J.-J., & vonNumbers, M. (2010). Temporal changes in the Island flora at different scales in the archipelago of SW Finland. *Applied Vegetation Science*, 13, 531–545.
- Harrell Jr, F. R. (2020). *rms: Regression Modeling Strategies*. R package version 6.0-1.
- Heaney, L. R. (2000). Dynamic disequilibrium: A long-term, large-scale perspective on the equilibrium model of Island biogeography. *Global Ecology and Biogeography*, 9, 59–74.
- Heinen, J. H., van Loon, E. E., Hansen, D. M., & Kissling, W. D. (2018). Extinction-driven changes in frugivore communities on oceanic islands. *Ecography*, 41, 1245–1255.
- Heleno, R., & Vargas, P. (2015). How do islands become green? *Global Ecology and Biogeography*, 24(5), 518–526.
- Hintze, C., Heydel, F., Hoppe, C., Cunze, S., König, A., & Tackenberg, O. (2013). D³: The dispersal and diaspore database - baseline data and statistics on seed dispersal. *Perspectives In Plant Ecology, Evolution and Systematics*, 15, 180–192.
- Jaccard, P. (1922). La chorologie selective et sa signification pour la sociologie vegetale. *Mémoires de la Société Vaudoise des Sciences Naturelles*, 2, 81–107.
- Järvinen, O. (1982). Species-to-genus ratios in biogeography: A historical note. *Journal of Biogeography*, 9, 363–370.
- Jöks, M., & Pärtel, M. (2019). Plant diversity in oceanic archipelagos: Realistic patterns emulated by an agent-based computer simulation. *Ecography*, 42, 740–754.
- Kavanagh, P. H., & Burns, K. C. (2014). The repeated evolution of large seeds on islands. *Proceedings: Biological Sciences*, 281, 20140675.
- Royal Botanic Gardens Kew. (2016). *Seed information database (SID)*. Version 7.1. Retrieved June 2016, from <http://data.kew.org/sid/>
- Kleyer, M., Bekker, R., Knevel, I., Bakker, J., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J. M., Klimeš, L., Klimešová, J., & Klotz, S. R. G. M. (2008). The LEDA Traitbase: A database of life-history traits of northwest European flora. *Journal of Ecology*, 96, 1266–1274.
- Klotz, S., Kühne, I., & Walter, D. (2002). *BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. - Schriftenreihe für Vegetationskunde 38*. Bundesamt für Naturschutz.
- Kohn, D. D., & Walsh, D. M. (1994). Plant species richness—The effect of Island size and habitat diversity. *Journal of Ecology*, 82, 367–377.
- Korvenpää, T., Van Numbers, M., & Hinneri, S. (2003). A mesoscale analysis of floristic patterns in the south-west Finnish archipelago. *Journal of Biogeography*, 30, 1019–1031.
- Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences*, 104, 5925–5930.



- Kreft, H., Jetz, W., Mutke, J., & Barthlott, W. (2010). Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. *Ecography*, 33, 408–419.
- Kreft, H., Jetz, W., Mutke, J., Kier, G., & Barthlott, W. (2008). Global diversity of Island floras from a macroecological perspective. *Ecology Letters*, 11, 116.
- Liu, J., Coomes, D. A., Hu, G., Liu, J., Yu, J., Luo, Y., & Yu, M. (2019). Larger fragments have more late-successional species of woody plants than smaller fragments after 50 years of secondary succession. *Journal of Ecology*, 107, 582–594.
- Lomolino, M. V. (1982). Species–area and species–distance relationships of terrestrial mammals in the Thousand Island region. *Oecologia*, 54, 72–75.
- Lomolino, M. V. (1990). The target area hypothesis: The influence of Island area on immigration rates of non-Volant mammals. *Oikos*, 57, 297.
- Lomolino, M. V., & Weiser, M. D. (2001). Towards a more general species–area relationship: Diversity on all islands, great and small. *Journal of Biogeography*, 28, 431–445.
- Long, J. A. (2020). *Jtools: Analysis and presentation of social scientific data*. R package version 2.1.0.
- Losos, J. B., & Ricklefs, R. E. (2010). *The theory of Island biogeography revisited*. Princeton University Press.
- Losos, J. B., & Schluter, D. (2000). Analysis of an evolutionary species–area relationship. *Nature*, 408, 847–850.
- Lüdecke, D. (2018). Ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, 3(26), 772.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of Island biogeography*. Princeton University Press.
- Matthews, T. J., Rigal, F., Triantis, K. A., & Whittaker, R. J. (2019). A global model of Island species–area relationships. *Proceedings of the National Academy of Sciences*, 9, 116(25), 12337–12342.
- McMaster, R. T. (2005). Factors influencing vascular plant diversity on 22 islands off the coast of eastern North America. *Journal of Biogeography*, 32, 475–492.
- Moeslund, J. E., Arge, L., Bøcher, P. K., Nygaard, B., & Svenning, J.-C. (2011). Geographically comprehensive assessment of salt-meadow vegetation–elevation relations using LiDAR. *Wetlands*, 31, 471–482.
- Morrison, L. W. (2010). Disequilibrium Island turnover dynamics: A 17-year record of Bahamian ants. *Journal of Biogeography*, 37, 2148–2157.
- Mortensen, M. F., Birks, H. H., Christensen, C., Holm, J., Noe-Nygaard, N., Odgaard, B. V., Olsen, J., & Lund Rasmussen, K. (2011). Lateglacial vegetation development in Denmark – New evidence based on macrofossils and pollen from Slotseng, a small-scale site in southern Jutland. *Quaternary Science Reviews*, 30, 2534–2550.
- Nagelkerke, N. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, 78, 691–692.
- Nogué, S., Santos, A. M. C., Birks, H. J. B., Björck, S., Castilla-Beltrán, A., Connor, S., de Boer, E. J., de Nascimento, L., Felde, V. A., Fernández-Palacios, J. M., Froyd, C. A., Haberle, S. G., Hooghiemstra, H., Ljung, K., Norder, S. J., Peñuelas, J., Prebble, M., Stevenson, J., Whittaker, R. J., ... Steinbauer, M. J. (2021). The human dimension of biodiversity changes on islands. *Science*, 372, 488–491.
- Oksanen, J. F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. M., Szoecs, E., & Wagner H. (2019). *vegan: Community Ecology Package*. R package version 2.5-6.
- Palmgren, A. (1915–1917). Studier över lövängsområdena på Åland. *Acta Soc. Fauna Flora Fennica*, 42, 1–634.
- Palmgren, A. (1921). Die Entfernung als pflanzengeographischer Faktor. *Acta Societatis pro Fauna et Flora Fennica*, 49, 1.
- Palmgren, A. (1925). Die Artenzahl als Pflanzengeographischer charakter sowie der Zufall und die säkulare Landhebung als Pflanzengeographische faktoren. *Acta Botanica Fennica*, 1, 1–142.
- Palmgren, A. (1927). Die Einwanderungswege der Flora nach den Ålandsinseln. *Acta Botanica Fennica*, 2, 1–198.
- Patiño, J., Weigelt, P., Guilhaumon, F., Kreft, H., Triantis, K. A., Naranjo-Cigala, A., Sólymos, P., & Vanderpoorten, A. (2014). Differences in species–area relationships among the major lineages of land plants: A macroecological perspective. *Global Ecology and Biogeography*, 23, 1275–1283.
- Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoğlu, Ç., Lloret, F., Buhek, C., Ojeda, F., Luna, B., Moreno, J. M., Rodrigo, A., Espelta, J. M., Palacio, S., Fernández-Santos, B., Fernandes, P. M., & Pausas, J. G. (2009). Fire-related traits for plant species of the Mediterranean Basin. *Ecology*, 90, 1420.
- Proença, V., & Pereira, H. M. (2013). Species–area models to assess biodiversity change in multi-habitat landscapes: The importance of species habitat affinity. *Basic and Applied Ecology*, 14, 102–114.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R foundation for statistical computing. <https://www.R-project.org/>
- Ricklefs, R. E., & Lovette, I. J. (1999). The roles of Island area per se and habitat diversity in the species–area relationships of four lesser Antillean faunal groups. *Journal of Animal Ecology*, 68, 1142–1160.
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.
- Scherber, C., Andert, H., Niedringhaus, R., & Tscharrntke, T. (2018). A barrier Island perspective on species–area relationships. *Ecology and Evolution*, ece3.4726.
- Schrader, J., Craven, D., Sattler, C., Cámara-Leret, R., Moeliono, S., & Kreft, H. (2021). Life-history dimensions indicate non-random assembly processes in tropical Island tree communities. *Ecography*, 44, 469–480.
- Simberloff, D. S., & Wilson, E. O. (1969). Experimental zoogeography of islands: The colonization of empty islands. *Ecology*, 50, 278–296.
- Sólymos, P., & Lele, S. R. (2012). Global pattern and local variation in species–area relationships. *Global Ecology and Biogeography*, 21, 109–120.
- Swenson, N. G. (2019). *Phylogenetic ecology: A history, critique, and remodeling*. University of Chicago Press.
- Triantis, K. A., Guilhaumon, F., & Whittaker, R. J. (2012). The Island species–area relationship: Biology and statistics. *Journal of Biogeography*, 39, 215–231.
- Triantis, K. A., Mylonas, M., Lika, K., & Vardinoyannis, K. (2003). A model for the species–area–habitat relationship. *Journal of Biogeography*, 30, 19–27.
- Triantis, K. A., Mylonas, M., Weiser, M. D., Lika, K., & Vardinoyannis, K. (2005). Species richness, environmental heterogeneity and area: A case study based on land snails in Skyros archipelago (Aegean Sea, Greece). *Journal of Biogeography*, 32, 1727–1735.
- Triantis, K. A., Vardinoyannis, K., Tsolaki, E. P., Botsaris, I., Lika, K., & Mylonas, M. (2006). Re-approaching the small Island effect. *Journal of Biogeography*, 33, 914–923.
- Valente, L., Illera, J. C., Havenstein, K., Pallien, T., Etienne, R. S., & Tiedemann, R. (2017). Equilibrium bird species diversity in Atlantic Islands. *Current Biology*, 27, 1660–1666.e5.
- vonNumbers, M., & van derMaarel, E. (1998). Plant distribution patterns and ecological gradients in the southwest Finnish archipelago. *Global Ecology and Biogeography Letters*, 7, 421–440.
- Weigelt, P., Kissling, W. D., Kisel, Y., Fritz, S. A., Karger, D. N., Kessler, M., Lehtonen, S., Lehtonen, S., Svenning, J. C., & Kreft, H. (2015). Global patterns and drivers of phylogenetic structure in Island floras. *Scientific Reports*, 5, 12213.
- Weigelt, P., & Kreft, H. (2012). Quantifying Island isolation—Insights from global patterns of insular plant species richness. *Ecography*, 36, 417–429.
- Wessberg, E., Løjtnant, B., Tranberg, H., Ernsten, O., & Hansen, A. (2011). *Homepage of the Danish Botanical Society*. Retrieved June 10, 2012, from <https://botaniskforening.dk/botanik/oflorae/>



- Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic Island biogeography. *Journal of Biogeography*, 35, 977–994.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D. A., François, R., Golemund, G., Hayes, A., Henry, L., Hester, J., & Kuhn, M. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686.

BIOSKETCH

Anna Walentowitz is interested in insular and global biogeographic patterns in the Anthropocene, with a special focus on invasion ecology. Claudia Troiano is interested in the study and management of biodiversity, particularly in rural and mountainous landscapes with a strong historical human presence. Manuel J Steinbauer investigates the processes that build and maintain biodiversity in human dominated systems and a pre-human past. Anders S. Barfod is interested in vegetation dynamics and in gaining insight into the processes that determine plant distribution patterns at various spatial scales.

Author contributions: ASB and MJS conceived the ideas; ASB, JBC and CT collected the data; AW, CT and MJS analysed the data; and AW and MJS, led the writing with contributions of all authors.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Walentowitz, A., Troiano, C., Christiansen, J. B., Steinbauer, M. J., & Barfod, A. S. (2022). Plant dispersal characteristics shape the relationship of diversity with area and isolation. *Journal of Biogeography*, 49, 1599–1608. <https://doi.org/10.1111/jbi.14454>