

Bioclimatic and physical characterization of the world's islands

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The Earth's islands harbor a distinct, yet highly threatened, biological and cultural diversity that has been shaped by geographic isolation and unique environments. Island systems are key natural laboratories for testing theory in ecology and evolution. However, despite their potential usefulness for research, a quantitative description of island environments and an environmental classification are still lacking. Here, we prepare a standardized dataset and perform a comprehensive global environmental characterization for 17,883 of the world's marine islands >1 km² (~98% of total island area). We consider area, temperature, precipitation, seasonality in temperature and precipitation, past climate change velocity, elevation, isolation, and past connectivity—key island characteristics and drivers of ecosystem processes. We find that islands are significantly cooler, wetter, and less seasonal than mainlands. Constrained by their limited area, they show less elevational heterogeneity. Wet temperate climates are more prevalent on islands, whereas desert climates are comparatively rare. We use ordination and clustering to characterize islands in multidimensional environmental space and to delimit island ecoregions, which provides unique insights into the environmental configuration and diversity of the world's islands. Combining ordination and classification together with global environmental data in a common framework opens up avenues for a more integrative use of islands in biogeography, macroecology, and conservation. To showcase possible applications of the presented data, we predict vascular plant species richness for all 17,883 islands based on statistically derived environment–richness relationships.

environmental regionalization | island biogeography | vascular plant diversity

Marine islands harbor a great part of our planet's biological and cultural diversity and provide ecosystem services to more than 500 million people (1). Existing estimates assign 3–3.6% of the Earth's land area to islands (2, 3) and their number exceeds 100,000, depending on threshold size (4). Islands vary greatly in geologic history, area, isolation, elevation, and climatic conditions (2, 5, 6). The complex interplay between islands' past and present environments and their isolated nature has produced biota that differ greatly among islands and between islands and mainlands (7). Islands are characterized by a high proportion of endemic species (3) and their unique biota are particularly susceptible to anthropogenic threats (1, 8, 9). Island research and conservation could make great progress with truly global analyses, but standardized data on key island biogeographic characteristics are currently lacking.

Biogeographic and macroecological research, and conservation planning, rely on spatially explicit data on both biodiversity and abiotic conditions (10). For instance, knowledge on environmental and compositional representativeness and irreplaceability is necessary for conservation prioritization (11, 12) and requires standardized data for all locations worldwide. Global data on climatic and other environmental drivers of ecosystem processes, and ecosystem responses like productivity and vegetation structure, are becoming increasingly available at increasing resolution (13), and knowledge on the biotic constituents of ecosystems has improved greatly (13, 14). The advent of such large

environmental and biodiversity datasets has opened up opportunities for global-scale analyses and, especially for mainlands, has facilitated significant progress in research over the past decade.

Although initially restricted to model archipelagos, such as Galapagos, Hawaii, and the Canaries, island research has inspired some of the most influential theories in ecology and evolution (5, 15–17). Recently, quantitative global analyses have also appeared (8, 18, 19) but have been restricted to a non-random subset of islands with available data. A synthesis of the macroecology of the world's islands is still missing. Although the large number, small size, and discrete boundaries of islands provide exciting research opportunities (17), the same qualities have hampered the compilation of standardized data. The United Nations Environment Programme Island Directory (20) was a first step toward a global overview, providing information on ~2,000 islands. More recently, scientific knowledge on physical and biological aspects of select islands and archipelagos was summarized (6) and the “Global Island Database” made available information for conservation and policy making (gid.unep-wcmc.org). Despite such first steps toward a global island dataset, a rigorous, standardized, and quantitative characterization of the world's islands is still lacking.

From a biological perspective, islands are inherently different from continental areas and drivers of these differences are key to understanding processes and patterns on islands (1). In island biogeographic theory, isolation and area are considered the most important drivers of island biodiversity (2, 15). Speciation predominantly occurs on large and isolated islands and large islands are more likely to maintain viable populations of many species (21–24). Isolation affects island biota in complex ways (22). For instance, the amount of surrounding landmass may determine the number of arriving propagules and the overwater distance may act as a dispersal filter causing compositional disharmony—an underrepresentation of certain taxonomic or ecological groups (25). However, a comprehensive framework for global island research requires going beyond classical island biogeographic determinants (26). Age and time–area dynamics are key predictors of the diversity of evolutionary arenas (27), and consequently island age and geology (e.g., volcanic vs. continental) represent core factors for understanding island biodiversity (23, 28). In addition, macroclimate, heterogeneity, and climate stability are known to influence endemism, assembly, and phylogenetic structure of island communities (19, 29–31).

Areas within which ecosystems share certain characteristics may be defined as “ecoregions” (32). Delineations may be based on biotic composition, evolutionary legacy, drivers of ecosystem

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processes (e.g., temperature), or measures of ecosystem responses (e.g., productivity; ref. 33). Biomes, e.g., describe regions of similar vegetation structure determined by temperature and precipitation (34–36). Often, criteria for delineations are not well defined. For instance, the widely used World Wildlife Fund ecoregion classification represents an expert-based assessment of both the distinctiveness of biotic assemblages and proxies such as vegetation structure (37). More quantitative classifications, made possible by the increasing availability of information, efficient algorithms, and computational power, have appeared recently (33, 38–40), but islands are often underrepresented or altogether excluded, due to their small size.

Here, we aim to provide a comprehensive environmental synopsis and classification of the world's islands. We (i) provide a comprehensive multivariate characterization and a standardized dataset of island bioclimatic and physical conditions; (ii) compare island and mainland environments; (iii) explore multivariate approaches for delineating environmental island ecoregions; (iv) provide general perspectives how this unique multivariate characterization may be used in island research and management; and (v) implement an example application by making environment-based predictions of vascular plant species richness on islands worldwide.

Results and Discussion

Island Environments. Our bioclimatic and physical characterization of the world's islands considered 85,122 marine islands smaller than Greenland. These islands comprise $\sim 7.84 \times 10^6$ km², or 5.3% of the Earth's land area, significantly exceeding previous estimates of 3–3.6% (2, 3). In total, 65,730 islands in the dataset are smaller than 1 km², but they make up only 0.17% of overall island area. Hence, island sizes show a strongly right-skewed distribution (17 islands >100,000 km²; Fig. S1). How many islands exist in total cannot be straightforwardly estimated. Fractal theory predicts island number to increase with decreasing minimum considered island area, up to millions of smallest islets and rocks (4). We focused on islands >1 km², which is biologically justifiable because on small islands speciation events and endemism are rare (21, 22) and stochastic forces drive

diversity patterns (41). Of 19,392 islands >1 km², 17,883 had sufficient environmental information for a detailed assessment of bioclimatic and physical conditions (Fig. 1 and Table S1). Together, they comprise $\sim 7.67 \times 10^6$ km², i.e., 5.2% of the Earth's land area and 97.8% of total island area, and serve as a solid baseline for an abiotic characterization of the world's islands.

Contrary to what some map projections suggest, Hawaii is not the most remote archipelago. The most remote islands belong to the Society and Austral Islands and Western Tuamotu (French Polynesia; Fig. 1B). Tahiti, $\sim 5,900$ km from the nearest mainland, is the largest of these islands. In terms of surrounding landmass (42), the most isolated islands lie east of Australia (from Macquarie Island to Fiji; Fig. 1C), including New Zealand and New Caledonia, islands of outstandingly high endemism richness (3). Assuming a decrease in sea levels of 122 m (43), about 75% of all islands were probably connected to a continent during the last glacial maximum (LGM) (Fig. 1D). Such land bridges could have allowed biotic exchange between and homogenization of the respective island and mainland assemblages. Isolated evolution on unconnected islands, in contrast, may have preserved unique assemblages, including relict endemics on old continental fragments and iconic adaptive radiations on volcanic archipelagos (17, 44).

Sixty-five percent of all islands are tropical. Annual mean temperature and temperature seasonality follow typical latitudinal trends (Fig. 1F and G). Past climate change velocity, i.e., the speed needed to track the mean annual change in temperature since the LGM [21,000 years before the present (y BP)], while accounting for variation in topographic complexity, is highest on North Atlantic islands (Fig. 1H), which is consistent with ref. 31. Precipitation is highest on tropical and highly elevated islands (Fig. 1I), with high intraarchipelago variation. For instance, within the Marquesas, only islands higher than 800 m receive rainfall exceeding 3,000 mm/y. Consequently, they harbor cloud and rain forests and differ from lower islands in composition and richness (45). In contrast, flat islands can be extremely dry. Precipitation seasonality is highest on tropical islands at western continental coasts (e.g., Isla Lobos de Tierra, Peru, and Cape Verde; Fig. 1J).

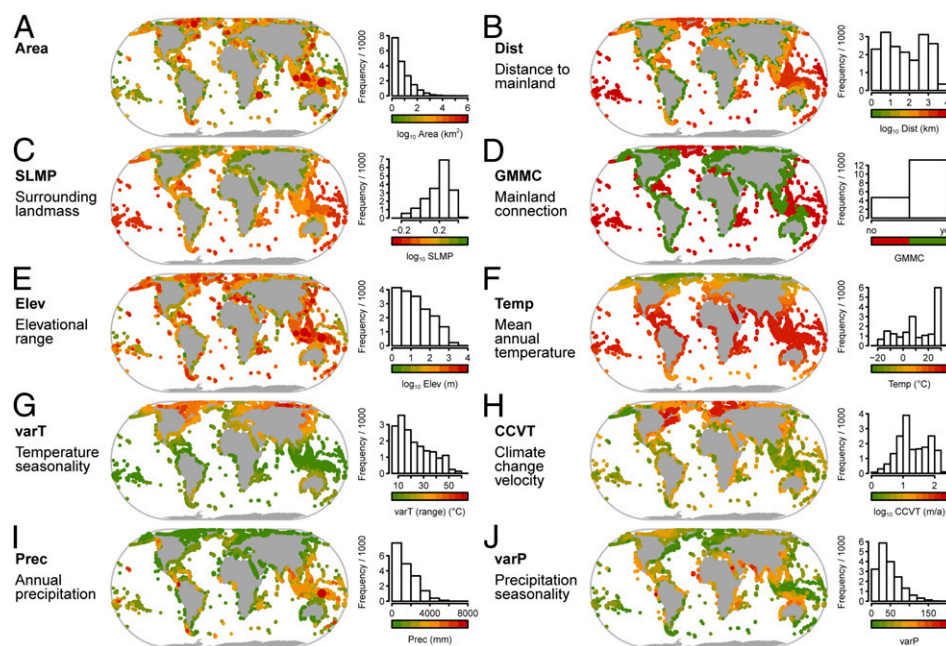


Fig. 1. Global patterns of key physical and bioclimatic variables on 17,883 marine islands >1 km². (A) Island area (*Area*), (B) distance to mainland (*Dist*), (C) surrounding landmass proportion (*SLMP*), (D) glacial maximum mainland connection (*GMMC*), (E) elevational range (*Elev*), (F) annual mean temperature (*Temp*), (G) temperature seasonality (*varT*), (H) climate change velocity in temperature (*CCVT*), (I) annual precipitation (*Prec*), (J) precipitation seasonality (*varP*). Points are plotted in order of decreasing frequency, i.e., islands with rare environments are plotted on top of islands with common characteristics if points overlap.

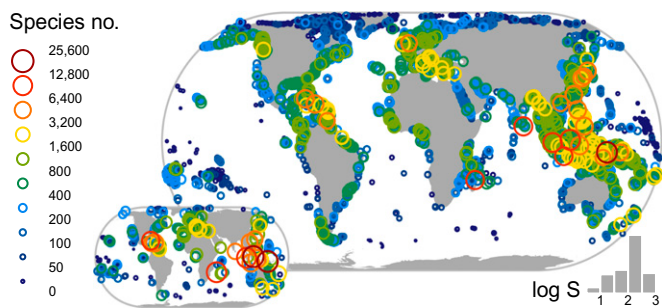


Fig. 5. Predictions of vascular plant species richness for 17,883 islands >1 km² (constituting $\sim 98\%$ of global island land area) worldwide based on generalized additive models and model averaging. Predictors include the 10 bioclimatic and physical variables presented here, richness of the nearest mainland region, and spatial position on the sphere. Circles were plotted in order of increasing species richness. The embedded map indicates the observed species richness of vascular plants for 475 islands used to train the model. The histogram shows the frequency distribution of \log_{10} species richness.

We identified islands of high past climate change velocity and areas where species may track future changes in a heterogeneous topography. Finally, human impact is higher on islands and land use-driven changes will still increase (3). An ecoregion framework may assist in assessing habitat loss and conversion and identifying areas of high representativeness, distinctiveness, and priority for nature conservation (11, 12).

Our approach is limited by the accuracy of the underlying bioclimatic and physical data (*SI Materials and Methods*) and because it is purely environment based. However, the richness models indicate that the environmental factors strongly relate to biogeographic factors. Once available at the global scale, biotic similarity could be used in combination with an abiotic characterization to quantitatively delimit island biogeographic regions that account directly for biogeographic history (37, 40). Until then, the data and approaches described here can serve as a baseline and source for developing and testing hypotheses, and for identifying islands of particular environmental uniqueness or representativeness and the predictions of vascular plant species richness can aid in identifying islands of outstanding biodiversity. The standardized dataset (*Dataset S1*) and quantitative nature of our characterization and ecoregionalization may contribute to more rigorous and reproducible approaches in island research and conservation.

Materials and Methods

Islands. We defined islands as landmasses surrounded by ocean and smaller than Greenland. This excludes freshwater islands. As geographic reference, we used the GADM database (www.gadm.org/version1), which includes 85,122 high-resolution island polygons. We focused on all 19,392 islands >1 km². Comparison with 90-m resolution elevation data (srtm.csi.cgiar.org) confirmed that these polygons include most islands >1 km² worldwide. For 17,883 islands, we could assemble complete environmental information. The 1,509 missing islands were distributed evenly across island-rich regions of the globe and were only slightly larger than 1 km² (Fig. S1).

Physical Variables. We considered five bioclimatic and five physical variables describing the exogenous physical environments of islands (33). Island area (*Area*) was calculated for each GADM polygon in cylindrical equal area projection. Although polygon area differs from actual surface area, which is influenced by island topography, it is an adequate approximation (26). As measures of isolation, we used the distance to the nearest mainland (*Dist*) and the proportion of surrounding landmass (*SLMP*). *Dist* was calculated as the shortest great circular distance between an island's mass centroid and the mainland coast. This metric is as good an isolation metric at a global scale as the distance from the island coast (42), but its calculation is computationally less demanding. Antarctica was not considered as mainland due to its permanent ice cover. We calculated *SLMP* as the sum of the proportions of landmass within buffer distances of 100, 1,000, and 10,000 km around the island perimeter. *SLMP* has been shown to be the best isolation metric to explain island plant diversity at a global scale (42). Unlike other

isolation metrics, *SLMP* accounts for coastline shape of large landmasses by considering only regions that extend into the measured buffers. As a coarse proxy for island geological history, we noted whether an island was connected to the mainland during the LGM (*GMMC*), assuming a sea level at 18,000 y BP of 122 m below the present level (43). More sophisticated geologic data are not available at reasonable spatial resolution, but *GMMC* differentiates well between oceanic and continental islands (Fig. 1D). We included the maximum elevation of each island as a measure of topographic complexity and a proxy for environmental heterogeneity (*Elev*). *Elev* relates to the number of available habitats as a result of differences between windward and leeward sites, temperature decrease with altitude, and high precipitation regimes in certain altitudinal belts (52). Elevation data at 30-s resolution was from ref. 53. For 1,891 small islands that did not fully enclose a 30-s raster cell, we applied a 1-km buffer to the island perimeter.

Bioclimatic Variables. For most islands, bioclimatic variables came from WorldClim (53). We used maximum values of annual mean temperature (*Temp*) and annual precipitation (*Prec*), as these are key drivers of ecosystem processes, vegetation structure (32), and species richness (19). Intraannual seasonality was quantified using the minimum annual temperature range (*varT*) and the minimum coefficient of variation in monthly precipitation (*varP*). We focused on extreme values rather than spatial means to capture the climatically most favorable part of each island. A region of French Polynesia and the Pitcairn Islands comprising 129 islands >1 km² and including important volcanic islands like the Marquesas, was not covered by WorldClim temperature data. We therefore modeled *Temp* and *varT* for these islands based on the strong correlation of sea surface and air temperatures of neighboring islands (*SI Materials and Methods*). We calculated climate change velocity in temperature (*CCVT*) since the LGM 21,000 y BP as the ratio between temporal change and contemporary spatial change in temperature at 30-s resolution and extracted mean values for each island (*SI Materials and Methods*) (31). Because of the higher uncertainty in paleoclimatic reconstructions of precipitation (31), we did not include climate change velocity in precipitation. We acknowledge the limitations of the bioclimate datasets, as the WorldClim model interpolates from weather station observations using latitude, longitude, and elevation (53). Climate predictions in regions with poor station density and varied topography have limited reliability (54).

Island Age. For 102 volcanic islands unconnected to the mainland during the LGM, we assembled island ages, an important determinant of species diversity and endemism (28), from primary research literature and compilations (e.g., ref. 6). Due to the small sample size, island age did not enter multivariate analyses but we assessed its relation to other variables.

Statistical Analyses. *Area*, *Elev* + 1, *Dist* + 1, *SLMP* + 0.5, and *CCVT* + 1 were \log_{10} -transformed to reduce skewness and to moderate extreme values. Small constants were added to avoid taking the logarithm of zero. We assessed spatial autocorrelation using Moran's I values. Collinearity was evaluated using pairwise correlations. Coefficients and significances were corrected for spatial autocorrelation following ref. 55. We performed PCAs of both including all standardized variables and for the following subsets: all variables but *Area* and *Elev*, contemporary bioclimatic variables only (*Temp*, *varT*, *Prec*, *varP*), and physical features only (*Area*, *Dist*, *SLMP*, *GMMC*, *Elev*).

To compare the environmental characteristics of islands and mainlands, we performed a PCA of all 17,883 islands and 42,985 equal area mainland grid cells spanning all continental areas worldwide (each 3,091 km² but covering less landmass in coastal areas). As input variables, we used all bioclimatic and physical variables not restricted to islands (*Elev*, *Temp*, *varT*, *Prec*, *varP*, and *CCVT*). We used kernel densities in PCA biplots as a measure of occupancy and correlated them among geologic units (all islands, islands connected to mainland at the LGM, unconnected islands, mainlands).

To delimit island regions of similar bioclimatic and physical conditions, we performed cluster analyses based on the 10 environmental variables and the variable subsets mentioned above. We used agglomerative hierarchical (UPGMA) and nonhierarchical clustering methods (PAM). UPGMA produces a cluster dendrogram representing the relatedness of the delimited regions. From the dendrogram, a preferred number of clusters can be inferred (56). PAM requires a specified number of clusters in advance and does not provide relationships among regions. However, PAM tends to delineate clusters of similar size and upper limits of within-group variance, preventing the creation of regions that greatly differ in within-region variance (38). Due to the strong collinearity of some variables, we used Euclidean distances on PCA axes as input distances; these are most appropriate because of the orthogonal nature of the PCA space (57). PCA axes were weighted by the square root of their eigenvalues to reduce the influence of less important

axes (57). We chose a number of clusters small enough for presentation and discussion based on the Caliński and Harabasz index (56).

Environment–Richness Model and Global Prediction. As example application of the integrated physical and bioclimatic island data, we produced species richness predictions for all 17,883 islands >1 km². The modeling approach builds on previous work (19, 42). For 475 islands, we collected numbers of native vascular plant species per island from floras, checklists and compilations (19, 42) (*SI Materials and Methods*). As predictor variables, we used the presented physical and bioclimatic variables, and vascular plant richness in the nearest mainland grid cell of the cokriging data in ref. 58 to reflect historical biogeographic influences on the available species pool. We used generalized additive models including penalized regression splines with up to three degrees of freedom, and an isotropic smooth of latitude and longitude on a sphere to account for spatial patterns in the response variable (47). We allowed tensor product interactions among *Area* and *Temp*, *Dist* and *SRML*, *Temp* and *Prec*, and *Area* and *Dist*. We made predictions based on multiple candidate models weighted

by model fit (46) and used 10-fold cross-validation to estimate prediction errors. Methods and results of alternative modeling approaches can be found in *SI Materials and Methods*, Fig. S7, and Table S5.

All bioclimatic and physical variables, ordination and clustering results, richness values of the nearest mainland grid cell, and predicted vascular plant species richness values per island are available in *Dataset S1* and at the Dryad Repository (dx.doi.org/10.5061/dryad.fv94v).

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