

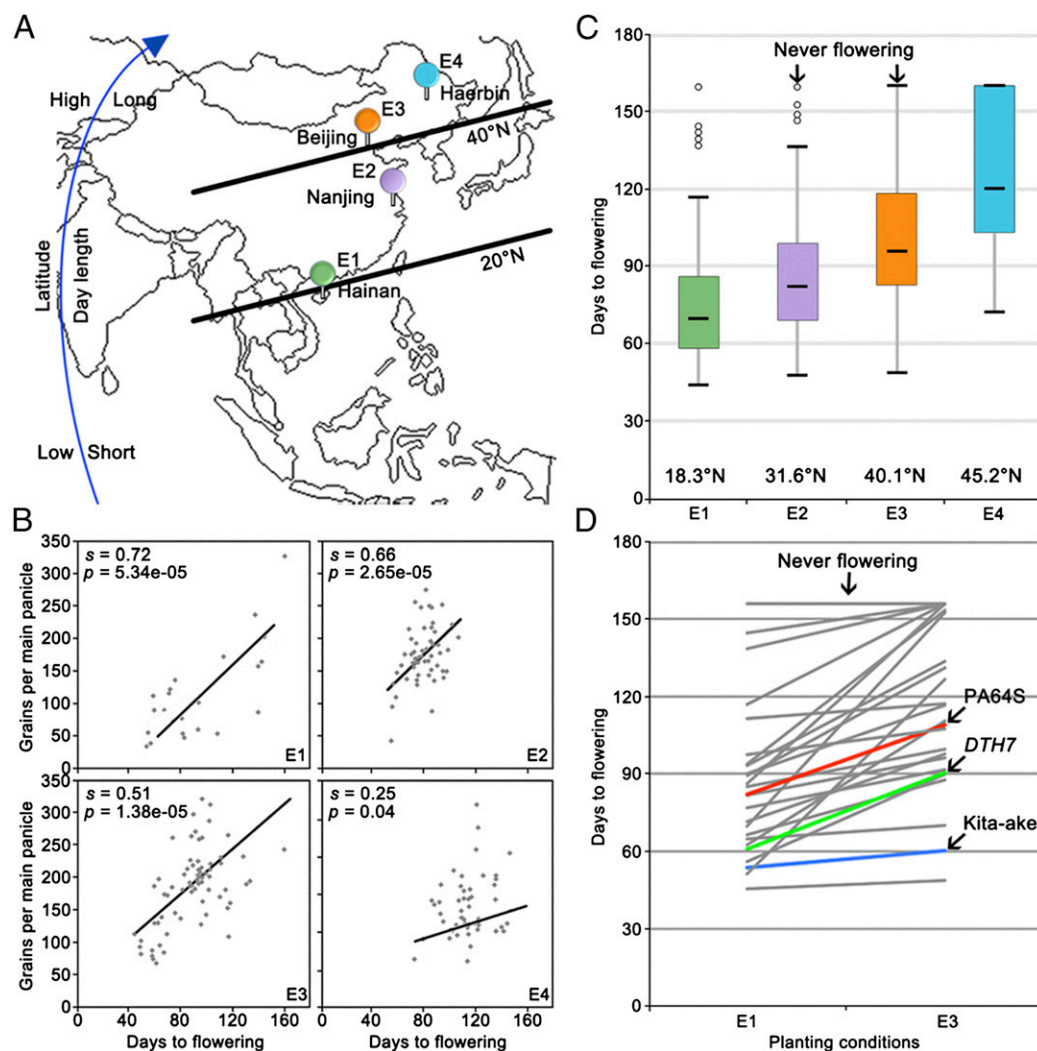
# Corrections

## AGRICULTURAL SCIENCES

Correction for “Days to heading 7, a major quantitative locus determining photoperiod sensitivity and regional adaptation in rice,” by He Gao, Mingna Jin, Xiao-Ming Zheng, Jun Chen, Dingyang Yuan, Yeyun Xin, Maoqing Wang, Dongyi Huang, Zhe Zhang, Kunngeng Zhou, Peike Sheng, Jin Ma, Weiwei Ma, Huafeng Deng, Ling Jiang, Shijia Liu, Haiyang Wang, Chuanyin

Wu, Longping Yuan, and Jianmin Wan, which appeared in issue 46, November 18, 2014, of *Proc Natl Acad Sci USA* (111:16337–16342; first published November 5, 2014; 10.1073/pnas.1418204111).

The authors note that the legend for Fig. 1 appeared incorrectly. The figure and its corrected legend appear below.



**Fig. 1.** Association between grain yield and flowering time in rice. (A) Geographic locations of four planting stations: E1, Hainan (18°30'N, 110°2'E); E2, Nanjing (31°56'N, 119°4'E); E3, Beijing (40°13'N, 116°13'E); and E4, Haerbin (45°20'N, 127°17'E). (B) Grains per main panicle is associated with flowering time. Grains per main panicle of a partial set of accessions were recorded under E1 to E4 conditions. The standardized coefficient was represented by  $s$ . Student's  $t$  tests were used to generate the  $p$  values. (C) Flowering time of 91 accessions in the core collections under E1, E2, E3, and E4 conditions. (D) Flowering time of a partial set of the core collection accessions under natural SDs (E1) and LDs (E3). Flowering time and grains per main panicle of each accession are presented as means  $\pm$  standard deviations ( $n = 20$ ).

www.pnas.org/cgi/doi/10.1073/pnas.1422341112

## NEUROSCIENCE

Correction for “Uridine adenosine tetraphosphate is a novel neurogenic P2Y1 receptor activator in the gut,” by Leonie Durnin, Sung Jin Hwang, Masaaki Kurahashi, Bernard T. Drumm, Sean M. Ward, Kent C. Sasse, Kenton M. Sanders, and Violeta N. Mutafova-Yambolieva, which appeared in issue 44, November 4, 2014, of *Proc Natl Acad Sci USA* (111:15821–15826; first published October 23, 2014; 10.1073/pnas.1409078111).

The authors note that a footnote indicating that Leonie Durnin, Sung Jin Hwang, and Masaaki Kurahashi contributed equally was omitted from the published article. The corrected author line and relevant footnotes appear below.

**Leonie Durnin<sup>2</sup>, Sung Jin Hwang<sup>2</sup>, Masaaki Kurahashi<sup>2</sup>,  
Bernard T. Drumm, Sean M. Ward, Kent C. Sasse,  
Kenton M. Sanders, and Violeta N.  
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## ECOLOGY, ENVIRONMENTAL SCIENCES

Correction for “Bioclimatic and physical characterization of the world's islands,” by Patrick Weigelt, Walter Jetz, and Holger Kreft, which appeared in issue 38, September 17, 2013, of *Proc Natl Acad Sci USA* (110:15307–15312; first published September 3, 2013; 10.1073/pnas.1306309110).

The authors note that on page 15308, right column, second full paragraph, line 1, “Sixty-five percent of all islands are tropical” should instead appear as “Sixty-five percent of all islands are nontropical.”

[www.pnas.org/cgi/doi/10.1073/pnas.1422548112](http://www.pnas.org/cgi/doi/10.1073/pnas.1422548112)

# 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 km<sup>2</sup> (~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 irreplacability 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](http://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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Data deposition: The data in Dataset S1 have been deposited in the Dryad Repository, [datadryad.org](http://datadryad.org) ([dx.doi.org/10.5061/dryad.fv94v](https://doi.org/10.5061/dryad.fv94v)).

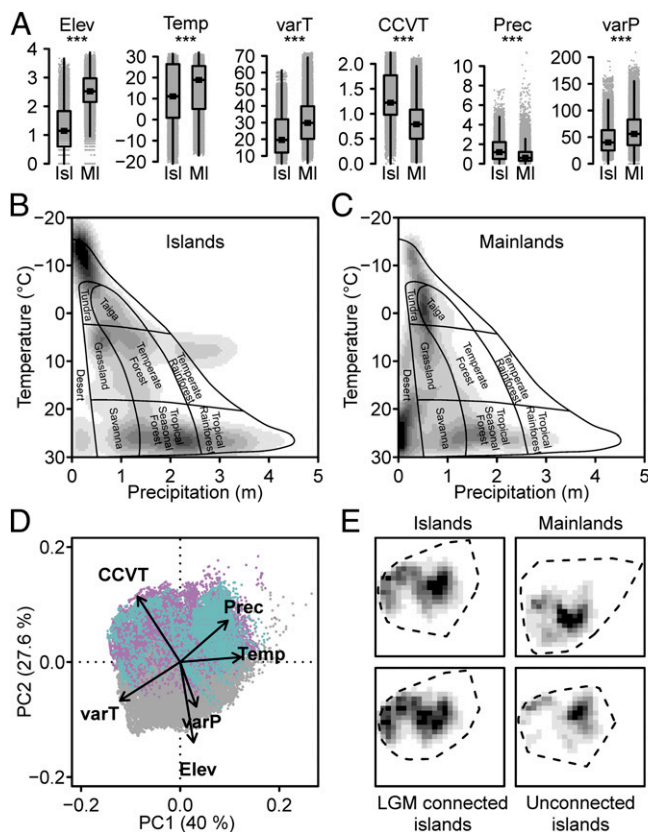
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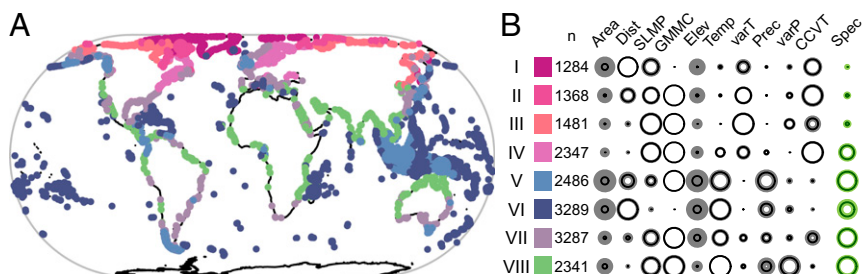
**Fig. 3.** Island vs. mainland comparisons. (A) Elevational range (*Elev*) (in  $\log_{10}$  meters), annual mean temperature (*Temp*) (in degrees Celsius), annual temperature range (*varT*) (in degrees Celsius), past climate change velocity in temperature (*CCVT*) [in  $\log_{10}$ (meters per year)], annual precipitation (*Prec*) (in meters), and variation in precipitation (*varP*) compared for 17,883 islands  $>1$  km<sup>2</sup> (Isl) and 42,985 equal area mainland grid cells (MI). Significance of differences was assessed using Mann–Whitney *U* tests (\*\*\**P* < 0.001). Boxes represent the interquartile range around the median; whiskers extend 1.5 times the interquartile range from the box. (B) Densities of islands and (C) mainland grid cells plotted onto Whittaker's scheme of biomes (35) delineated on the basis of *Temp* and *Prec*. (D) PCA for 4,676 oceanic islands (cyan), 13,207 continental islands (magenta), and mainland grid cells (gray). (E) Kernel densities of geologic subsets along the first two PCA axes.

for the world's island environments, the specific outcome is contingent on the number of groups chosen and the clustering algorithm. Using the unweighted pair-group method with arithmetic mean (UPGMA) instead of PAM produced groups of vastly different sizes (1–7,092 islands per cluster compared with 1,284–3,289 islands per cluster; Fig. S6), highlighting the methodological sensitivity of the clustering approach. The application of environment-based regionalizations is also limited by the gradual nature of most environmental changes, which compromises the idea of strict distinctions. Multivariate measures of environmental similarity based

on PCA analyses and as mapped in Fig. 2 may represent a more appropriate and powerful tool to account for gradual changes when analyzing and visualizing regional affinities. We suggest carefully checking the results of both the ordination and clustering steps.

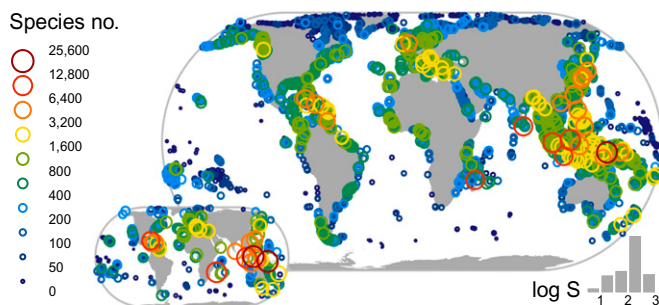
**Richness Predictions.** To showcase possible applications of the presented data and multivariate framework, we used it to predict the species richness of native vascular plants on all 17,883 islands  $>1$  km<sup>2</sup>. Specifically, we used a multimodel approach (46) and included as predictors the 10 presented bioclimatic and physical variables, richness of the nearest mainland region, and spatial position on the sphere (Fig. 5 and Table S5). The averaged model achieved remarkably strong fits with observed richness on the 475 islands used for training (Fig. S7; pseudo-*R*<sup>2</sup> = 0.94; averaged mean error based on 10-fold cross-validation, 0.031; not accounting for spatial nonindependence). The South East Asian Archipelago, the Caribbean, and the Mediterranean emerged as richness centers, attributable to their many large islands, (sub) tropical climates, low degrees of isolation, and high regional mainland diversity (Fig. 5). Oceanic islands were on average less diverse than continental islands with only few exceptionally diverse islands (Figs. 4 and 5). The generalized additive modeling approach presents a flexible way to account for multiple non-linear effects and complex interactions, as well as spatial richness variation (47). However, the model underestimated species richness on some large, tropical islands (compare Fig. S7) and overestimated it on others (e.g., Britain). Although the model captures the interplay of bioclimatic and physical drivers of insular plant species richness, the predictions only account for the variables selected and do not mechanistically address the historical biogeography of the different plant clades found on islands. We therefore caution against their use without contemplation. Nevertheless, the predictions give a first global overview of vascular plant species richness on islands and may provide a good baseline prediction against which to test ecological and evolutionary processes in island biogeography.

**Perspectives.** In contrast to alternative global frameworks (39), our study specifically focuses on islands. It represents a first step toward a thorough characterization of the world's islands for island research and conservation. The data may help to address questions in ecology and evolution, such as whether the unique diversity of islands and speciation patterns are due to isolation and lack of gene flow or whether island evolution differs from mainland evolution due to environmental differences (48). The framework also has great potential for island conservation. Island biota are particularly threatened, by biological invasions, habitat loss, and changing climate (1, 3, 8, 9). The majority of historically recorded vertebrate extinctions occurred on islands and 39% of species facing imminent extinction are island species (49). Island communities are highly susceptible to invasion-induced extinction and biotic homogenization (8, 50). Assessing environmental similarity may help to connect potential source and target areas for invaders and aid in proactive measures. Further, climate change particularly affects island ecosystems due to sea level rise and limited space for range shifts (1, 9, 51).



**Fig. 4.** PAM clustering of weighted PCA axes for 17,883 islands  $>1$  km<sup>2</sup> based on eight environmental variables (all except *Area* and *Elev*). Colors in the map (A) are calculated as mean RGB values of all islands per cluster based on the PCA in Fig. 2E. Points were plotted in decreasing order of *Area*. Circles in B indicate variable characteristics within the clusters: circle, arithmetic mean; shaded ring, SD. Abbreviations follow Fig. 1. *Spec* indicates predicted vascular plant species richness.





**Fig. 5.** Predictions of vascular plant species richness for 17,883 islands  $>1 \text{ km}^2$  (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](http://www.gadm.org/version1)), which includes 85,122 high-resolution island polygons. We focused on all 19,392 islands  $>1 \text{ km}^2$ . Comparison with 90-m resolution elevation data ([srtm.csi.cgiar.org](http://srtm.csi.cgiar.org)) confirmed that these polygons include most islands  $>1 \text{ km}^2$  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  $1 \text{ km}^2$  (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  $>1 \text{ km}^2$  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 bioclimatic 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  $3,091 \text{ km}^2$  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 km<sup>2</sup>. 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](https://doi.org/10.5061/dryad.fv94v)).

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