

Global patterns and determinants of vascular plant diversity

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Plants, with an estimated 300,000 species, provide crucial primary production and ecosystem structure. To date, our quantitative understanding of diversity gradients of megadiverse clades such as plants has been hampered by the paucity of distribution data. Here, we investigate the global-scale species-richness pattern of vascular plants and examine its environmental and potential historical determinants. Across 1,032 geographic regions worldwide, potential evapotranspiration, the number of wet days per year, and measurements of topographical and habitat heterogeneity emerge as core predictors of species richness. After accounting for environmental effects, the residual differences across the major floristic kingdoms are minor, with the exception of the uniquely diverse Cape Region, highlighting the important role of historical contingencies. Notably, the South African Cape region contains more than twice as many species as expected by the global environmental model, confirming its uniquely evolved flora. A combined multipredictor model explains $\approx 70\%$ of the global variation in species richness and fully accounts for the enigmatic latitudinal gradient in species richness. The models illustrate the geographic interplay of different environmental predictors of species richness. Our findings highlight that different hypotheses about the causes of diversity gradients are not mutually exclusive, but likely act synergistically with water–energy dynamics playing a dominant role. The presented geostatistical approach is likely to prove instrumental for identifying richness patterns of the many other taxa without single-species distribution data that still escape our understanding.

biodiversity | historical contingency | latitudinal gradient | macroecology | species richness

Geographic patterns of species distributions are central to ecology (1–7). Progress toward more general and, importantly, global models of gradients of species richness to date has been hampered by the many species that remain only poorly documented in their geographic occurrence or altogether unknown (8). For an understanding of the global distribution of diversity, plants might be of particular relevance. Plants comprise some 300,000 species, are key structural elements of terrestrial ecosystems, and are the basis of all terrestrial food webs. High plant diversity is likely associated with high biotic heterogeneity and thus a higher potential for specialization in various animal groups (9). Generally, medium to strong positive relationships between producer and consumer diversity have been found (10–12). Plants may thus play a central role as an indicator group; under this assumption, their richness pattern has already been used extensively for global-scale conservation priority setting (13).

Recently, considerable progress has been made toward documenting broad-scale patterns of plant richness (11, 14–21). In general, two different data-type approaches are possible to map and analyze global richness gradients (22). First, studies may be based on single-species occurrence data in the form of locality records or expert range maps (23–25). Unfortunately, this approach is limited by the relatively small fraction of all species for which such data are available. Second, and consequently, a

single-species approach for mapping and analyzing global distributions of many speciose groups, such as vascular plants, will long remain elusive. Thus, the method of choice is analyzing the species-richness information for geographic units with floras that have been well described (11, 21, 22). This method offers a powerful approach to understanding the variability of plant species richness at a global scale.

A number of studies have shown a remarkably strong association between contemporary climate and species richness (4, 5, 7, 11, 16, 26–28). According to the “water–energy dynamics hypothesis,” species richness at higher latitudes is controlled by the availability of ambient heat, whereas, in the thermally suitable tropics, water- and humidity-related variables are the main driving factors (4, 5, 28). Alternatively or additionally, the sensitivity of most plants to frost or drought may constrain their richness outside warm and humid regions (5, 29). Another set of hypotheses states that habitat heterogeneity governs species-richness gradients by local and regional species turnover (30, 32). Third, historical/evolutionary hypotheses attribute species-richness gradients to geographic differences in the geological and climatic history, such as tectonic movements, uplift of mountain ranges, long-term climatic stability, or Pleistocene cooling and dryness. These historic factors may cause divergent rates of diversification (32–35). Recently, water- and energy-related variables have been found to be dominant predictors of global angiosperm family richness (27). Whether this would question a major role for historical factors has been debated (35). To date, relative roles of potential environmental and historical drivers of species diversity lack scrutiny.

Here, we present an analysis of geographic patterns and putative macroecological determinants of vascular plant diversity at the species level and with a global scope. Our analysis is based on an exhaustive data set of 1,032 regions worldwide that has been used to produce expert opinion-based continental to global maps of plant species richness (11, 14, 17, 21). We use both nonspatial and spatial (controlling for spatial autocorrelation) modeling techniques to test, in turn, the predictive potential of variables representing different hypotheses. We proceed to develop a combined multipredictor model and use it in conjunction with geostatistical techniques to predict vascular plant diversity across the whole world. We thereby outline a general geostatistical approach to capture the richness gradients of the many less studied groups of organisms that still escape our understanding.

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Abbreviations: AIC, Akaike information criterion; GLM, generalized linear model; PET, potential evapotranspiration; SLM, spatial linear model.

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Table 1. Results of GLM and SLM for selected predictor variables and species richness of vascular plants

Hypothesis and model	GLM				SLM			
	<i>t</i>	Deviance, %	AIC	Moran's <i>I</i>	<i>z</i>	Deviance, %	AIC	Moran's <i>I</i>
NULL	—	—	738	0.43	—	39.2	306	—
AREA	8.5	6.6	669	0.53	20.2***	57.4	−24	−0.02
Energy								
PET	14.2	25.4 (16.3)	439 (556)	0.34	6.9***	58.7 (40.6)	−72 (265)	−0.02
TEMP	9.8	16.9 (8.5)	551 (648)	0.37	13.6**	57.3 (39.1)	−22 (303)	−0.02
Water								
PRE	17.6	35.9 (23.2)	283 (467)	0.33	11.1***	63.9 (44.1)	−216 (200)	−0.03
WETDAYS	8.9	16.5 (7.2)	556 (663)	0.43	9.1***	64.2 (43.8)	−196 (228)	−0.03
Water–energy								
AET	20.3	41.4 (28.6)	191 (391)	0.28	13.1***	63.8 (44.2)	−224 (187)	−0.02
WAT-ENER	20.2	41.3 (28.4)	193 (394)	0.29	12.8***	64.5 (45.4)	−241 (169)	−0.02
PET + WETDAYS		51.1 (34.9)	6 (299)	0.24		65.8 (46.1)	−296 (145)	−0.02
PET	20.9	34.6 (27.7)			11.5***			
WETDAYS	17.1	25.7 (18.5)			11.9***			
PET × WETDAYS		52.6 (36.8)	−24 (270)	0.21		65.8 (46.1)	−297 (143)	−0.02
PET	−3.9	34.6 (27.7)			−0.8			
WETDAYS	−4.6	25.7 (18.5)			−1.3			
PET:WETDAYS	5.6	1.5 (1.9)			1.99*			
Heterogeneity								
TOPOVEG	20.3	28.7 (28.6)	392 (392)	0.50	24.4***	63.9 (61.9)	−206 (−161)	−0.03
TOPO	17.2	24.8 (22.4)	447 (478)	0.47	19.5***	64.2 (55.9)	−208 (−16)	−0.03
VEG	13.4	20 (20)	512 (510)	0.50	20.9***	63.9 (61.9)	−116 (−57)	−0.03
Structure								
STRUCT	14.5	29.5 (14.5)	381 (549)	0.30	5.7***	60 (40.1)	−103 (279)	−0.03
History								
KINGDOM	—	20.4 (13.1)	505 (605)	0.35	—	57.8 (39.7)	−33 (296)	−0.02
Others								
BIOME	—	46.4 (30.2)	120 (391)	0.18	—	62.4 (42.3)	−155 (248)	−0.02
LAT	−12.4	22.4 (13)	480 (595)	0.36	−5.6***	58.2 (40)	−57 (280)	−0.02

Species richness and all continuous predictor variables (except for VEG, TOPO, and TOPOVEG) were log₁₀-transformed. Null model: deviance = 123.01; AIC = 737.61; *n* = 1,032. Values in parentheses refer to models without control for area. Because GLMs do not remove spatial autocorrelation from the residuals, significance levels are not reported. High percentage of explained deviance in single predictor SLM is mostly due to the strong influence of spatial trend term. SLMs leave no significant spatial autocorrelation in the residuals (all global Moran's *I* have *P* > 0.05). PRE, mean annual precipitation [millimeters per year (mm/a)]; WAT-ENER, water–energy model according to ref. 36; KINGDOM, floristic kingdom membership; BIOME, biome membership; LAT, absolute latitude. *, *P* < 0.05; ***, *P* < 0.001.

Results and Discussion

The well known species–area relationship explains plant richness at local to regional scales (36). Interestingly, even across a variation of four orders of magnitude in our data set, area *per se* is a relatively weak predictor of species richness and explains only 6.6% of the global variation of plant species richness (Table 1). However, the explanatory power of area dramatically increases when spatial autocorrelation is explicitly modeled (57.4% deviance). This finding indicates strong neighborhood effects, which are also observed for subsequent environmental predictors [Table 1 and supporting information (SI) Table 3]. Furthermore, we find that regional spatial heterogeneity (measured as the number of vegetation types, elevational belts, or especially as a variable combining both) is a strong predictor of plant richness and is able to account for the effect of area (Table 1).

Among individual climatic variables, average annual temperature is thought to be of particular importance for ectothermic clades, given its exponential effect on rates of energy flux and thus, potentially, rates of biological interaction and diversification (3, 37). Although there is a significant positive effect of average annual temperature (TEMP) on vascular plant species richness (8.5% deviance; Table 1), there are indications for a quadratic rather than linear trend [Δ AIC = 25; where Δ AIC indicates the difference between the Akaike information criterion (AIC) of the model of interest and the AIC of the best fitting

model]. Under the generally untested assumption of uniform total abundance of individuals across space, the species–richness extension of the metabolic theory of ecology predicts a slope of 9.0 between the inverse of temperature (1,000/K) and the natural logarithm of species richness (37), which is very different from the one observed here [$\ln(\text{richness}) = 13.88 - 1.89 \text{ temperature}^{-1}(1,000/\text{K})$; test for difference in slope: *t* = 54.33; *P* < 10^{−15}].

Actual evapotranspiration emerges as the strongest single climatic predictor [28.6% deviance generalized linear model (GLM); Table 1]. Mean annual net primary productivity yields somewhat poorer fits than actual evapotranspiration (26.7%; Δ AIC = 28). Water–energy models that include interaction terms tend to have stronger explanatory power than those with only main effects confirming the important interdependence of these determinants. Of all potential combinations of energy-related variables and water-related variables, the full interaction model including potential evapotranspiration (PET) and the annual number of days with rainfall (WETDAYS, a variable that encapsulates both amount and temporal occurrence of precipitation) is the strongest (36.8% deviance). Other variable combinations to quantify the water–energy interaction (27, 38) yield significantly poorer fits (Δ AIC > 44). Visual inspection and split-line analyses of the relationship between PET and species richness indicate a threshold at 505-mm PET, above which the



Brazil, Northern Borneo, and New Guinea) (14, 17). Astonishingly, the most species-rich grid cell according to our combined model (situated between Colombia and Ecuador; Fig. 3b) has already been identified as such by Alexander von Humboldt (47) 200 years ago in the parlance of his time:

This portion of the surface of the globe affords in the smallest space the greatest possible variety of impressions from the contemplation of nature. . . . There, the different climates are ranged the one above the other, stage by stage, like the vegetable zones, whose succession they limit; and there the observer may readily trace the laws that regulate the diminution of heat, as they stand indelibly inscribed on the rocky walls and abrupt declivities of the Cordilleras.

Over the last decades, much controversy has arisen from the ambition to find one single factor that explains the enigmatic latitudinal gradient in species richness. Our findings demonstrate that different hypotheses are not mutually exclusive and core drivers likely act synergistically. Furthermore, our findings illustrate the significant advance that spatial analysis techniques applied to even megadiverse taxa at the global scale allow to both improve conceptual understanding as well as the quantitative knowledge base for conservation of yet understudied taxa. The challenge now is to close the many alarming taxonomic and geographic gaps in data availability that, surely to Humboldt's dismay, still exist.

Materials and Methods

Richness Data. We analyzed the species richness of vascular plants (i.e., ferns, gymnosperms, and angiosperms) across 1,032 geographic units worldwide (Fig. 3a). Geographic units represent natural (e.g., mountain ranges, desert, and biogeographic provinces) or political units (e.g., countries, provinces, and national parks) and were derived from floras, checklists, and other literature sources (refer to ref. 46 for a full list of references). The data set was originally assembled to produce expert opinion-based global maps of plant species richness (11, 14, 17, 19, 46) and continental geostatistical (16, 48, 49) analyses. The original data set consists of >3,300 species-richness accounts referring to >1,800 geographic units. We excluded oceanic islands because isolation or geological age play a major role in the assembly of island floras (50). Furthermore, we excluded geographic units with an area of <10 km² and >300,000 km² to avoid spatially overlapping units. The data set covers almost the full spectrum of the global variation in abiotic conditions and includes all major biomes and floristic kingdoms.

Putative Determinants. We tested 40 variables as potential determinants of species richness (see SI Table 3 for full descriptions and references of all examined variables). Climatic variables and net primary productivity data were derived from interpolated, digitally available global data sets. The net primary productivity data set represents an average of 17 different global models (see ref. 51 for details). Mean values were extracted across all 1,032 investigated geographical units in ArcINFO (ESRI, Redlands, CA). Water–energy dynamics received particular attention in our analyses. We analyzed the predictive power of variables or variable combinations that have been previously reported to be strong predictors of plant richness (4, 27, 38) as well as all other possible combinations of energy-related and water-related variables. To analyze the potential effects of historical contingencies, we included floristic kingdom membership as a further variable (43). When simultaneously controlling for environmental dissimilarity of core predictors, deviations in species richness from the global environmental trend may point to an additional influence of idiosyncratic historical events on species richness

(40, 52). We also tested different variables describing habitat heterogeneity. The number of 300-m elevational belts per geographic unit (range of elevation divided by 300; TOPO) was calculated as a proxy of topographical complexity (31) by using the GTOPO-30 digital elevation model. Furthermore, the number of different vegetation types (VEG) and soil types (SOIL) occurring in a geographic unit were counted. We additionally created the combined variable TOPOVEG (TOPO + VEG) because global land cover data tend to underestimate changes along elevational gradients. As a measure of space use of the vegetation, all biomes were ranked according to their three-dimensional structural complexity (STRUCT). This measure varies from one (desert and tundra) to six (tropical broadleaf forest) along an integer scale. Variables were assigned to different categories corresponding to different hypotheses of species-richness gradients.

GLM Analyses. First, we performed GLMs to analyze potential single predictors of species richness. In a second step, more complex models were created (compare Tables 1 and 2 and SI Table 4). The fit of individual models is reported by using the proportion of deviance explained [deviance = $-2 \times$ maximized log-likelihood; percentage deviance explained = $(100 - \text{null deviance} / \text{residual deviance}) \times 100$], because that makes GLM and SLM results directly comparable. The best single predictor or combination of predictors from each category was included into a combined multipredictor model. The goodness-of-fit in relation to the model complexity was evaluated by using the AIC, which incorporates the maximized log-likelihood of the model and a term that penalizes models with greater complexity (53). Model selection was then based on ΔAIC , which is the difference between the AIC of the model of interest and the AIC of the best fitting model (53).

Spatial Analyses. Spatial autocorrelation of species richness and predictor variables is a general feature of macroecological data sets (54). It inflates type I errors of traditional statistical tests and might affect parameter estimates (55). Because spatial autocorrelation also is present in the data set analyzed here, we performed simultaneous autoregressive models. Three different simultaneous autoregressive model types (lagged-response, lagged-mixed, and spatial error) were evaluated with different neighborhood structures and spatial weights (lag distances between 200 and 2,000 km, weighted and binary neighborhood coding). Final model selection was based on the reduction of spatial autocorrelation in the residuals and the minimization of AIC values. Simultaneous autoregressive models of the spatial error model type with a lag distance of 800 km and weighted neighborhood structure accounted best for the spatial structure in the analyzed data set. Spatial statistics were performed with the “spdep” library in the R software package (56). We assessed spatial autocorrelation in model residuals by using Moran's *I*, which can be considered a spatial equivalent to Pearson's correlation coefficient and normally varies between 1 (positive autocorrelation) and -1 (negative autocorrelation). The expected Moran's *I* value for lacking spatial autocorrelation is close to 0 (57). Spatial Moran's *I* correlograms for the response variable as well as for the GLM and SLM residuals are provided in SI Fig. 5.

Global Predictions. We derive global predictions of plant richness across an equal area grid of $\approx 110 \times 110$ km (12,100 km²; approximating an area of 1° latitude \times 1° longitude near the equator) (Fig. 3b). We first make predictions based on the parameter estimates of the combined GLM and by using the same predictor variables for the global grid. This approach does not account for the spatial structure in the data except for what is dictated by the predictor variables. In the absence of richness

data for unsampled neighboring locations, the incorporation of the spatial autocorrelation signal when predicting into unsampled areas is not trivial. We used a two-level approach. First, we applied the geostatistical interpolation technique of ordinary kriging, which is commonly applied in other disciplines, such as mining, meteorology, and soil research (57). This approach interpolates between sampled quadrats exclusively according to the spatial dependence of the response variable and ignores underlying environmental gradients but has the advantage of an exact interpolation method at sampled locations (Fig. 3c). Second, we link this limited approach with the GLM-based environmental model by using ordinary cokriging, a commonly applied technique to enhance interpolation estimates (57). Whereas the former considers only the spatial dependence of the

response variable, the latter also accounts for the environmental covariation. The resulting global species-richness map (Fig. 3d) accounts for both environmental gradients and underlying spatial trends in the richness of plants. Geostatistical analyses were performed with the Geostatistical Analyst extension in ArcGIS (ESRI).

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