

# 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

**G**eographic 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 log<sub>10</sub>-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.

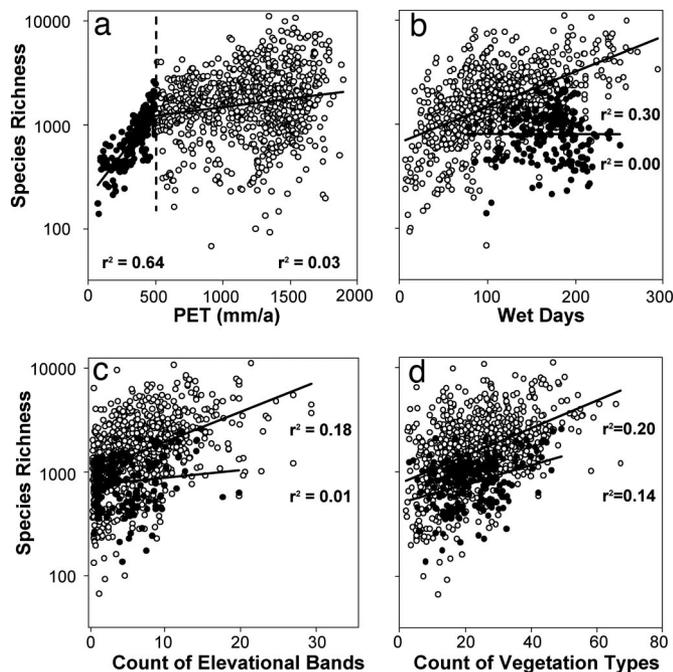
## Results and Discussion

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 [ $\Delta$ AIC = 25; where  $\Delta$ 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<sup>−15</sup>].

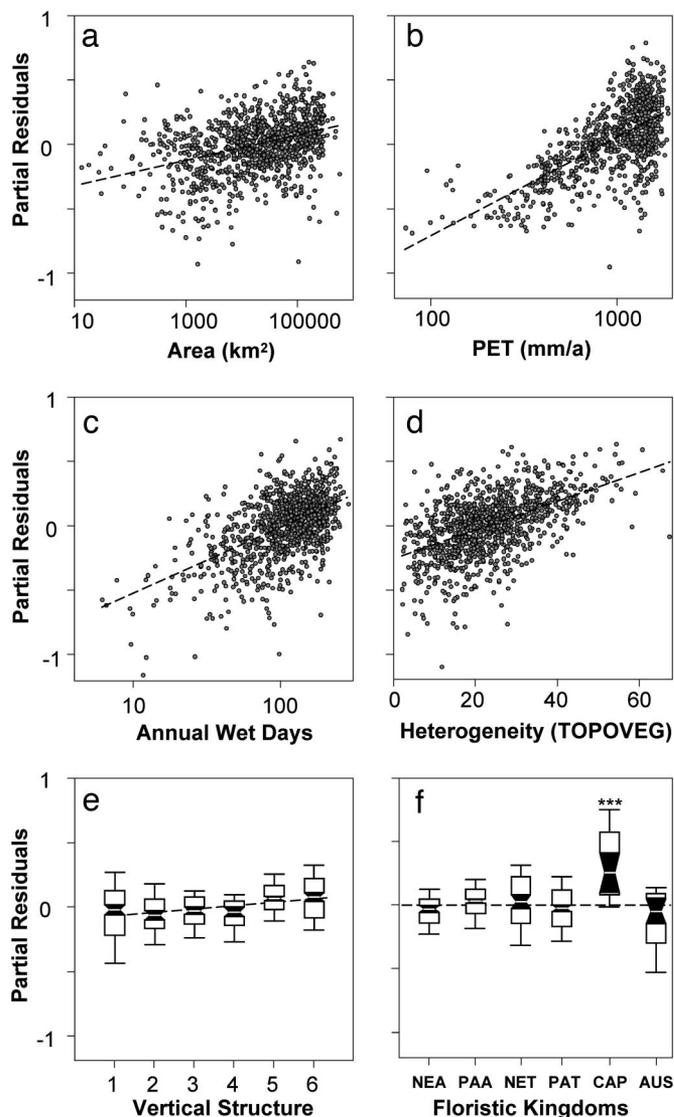
Actual evapotranspiration emerges as the strongest single climatic predictor [28.6% deviance generalized linear model (GLM); Table 1]. Mean annual net primary productivity yields somewhat poorer fits than actual evapotranspiration (26.7%;  $\Delta$ AIC = 28). Water–energy models that include interaction 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 ( $\Delta$ 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



**Fig. 1.** Relationship between environmental predictors and species richness of vascular plants in low- and high-energy regions. Species richness is standardized to 10,000 km<sup>2</sup>. (a) The effect of PET [millimeters per year (mm/a)] on species richness. A close association is observed in regions with <505 mm/a PET (filled circles), whereas in regions with higher energy input (open circles) the relationship is not significant (breakpoint confirmed by split-line regression). (b–d) Also shown are relationships for wet days (b), topographical complexity measured as the number of elevational bands (c), and heterogeneity measured in number of vegetation types per region (d).

relationship between species richness becomes largely independent from further increasing annual energy input (Fig. 1a). Above the same breakpoint, the number of wet days, a nonsignificant predictor in low-energy regions, assumes strong predictive power (Fig. 1b), highlighting that water constrains richness only in high-energy regions (4). A similar interaction occurs with topographical complexity (Fig. 1c), but not habitat heterogeneity as such (Fig. 1d). The interaction with topography is qualitatively similar to previous findings for North American mammals (39) but with a breakpoint at much lower energy levels (505- vs. 1,000-mm PET). This finding strongly points to the different energetic and physiological constraints between these two groups (ectothermic vs. endothermic). These differential constraints may have affected rates of diversification and range limits of species. Determinants of species richness might change with spatial scale (31), and we therefore test for interactions between area and all predictor variables. Despite the large variation in areas, no significant effects emerge ( $\Delta$ AIC between 0.3 and 2.7), corroborating the validity of our model results across a wide range of scales.

Historical effects, i.e., regional differences in rates of past speciation, extinction, and dispersal, are notoriously difficult to quantify and often covary with contemporary environment and physiography. Topographic heterogeneity often is associated with a high potential for speciation during past periods of climate change (25, 34, 40) or during a recent uplift of mountain ranges, such as the Andes or Himalaya (25, 41, 42). We already noted a strong effect of topographic complexity. An alternative way to capture regional histories is to compare historically distinct biotas composed of almost completely nonoverlapping taxa—i.e., realms or, in our case, six floristic kingdoms (KINGDOM; largely following ref. 43), which may be considered as statistical



**Fig. 2.** Partial residuals plots for all variables included in the combined model of global plant richness (compare Table 2). These plots show the effects of a given variable when all others in the model are statistically controlled for. (a–e) Hatched lines partial fits. (e and f) Boxes indicate second and third quartiles, black notches denote 95% confidence intervals, and whiskers indicate 10th and 90th percentiles. NEA, Nearctic; PAA, Palaearctic; NET, Neotropic; PAT, Paleotropic; CAP, Cape; AUS, Australis. Note high partial residuals of the Cape floristic kingdom after controlled-for environmental differences (\*\*\*, significant at  $P < 0.001$ ; Tukey post hoc test). Specifically, a partial residual plot is a plot of  $r_i + b_k \times i_k$  vs.  $x_{ik}$ , where  $r_i$  is the ordinary residual for the  $i$ th observation,  $x_{ik}$  is the  $i$ th observation of the  $k$ th predictor, and  $b_k$  is the regression coefficient estimate for the  $k$ th predictor.

replicates. Kingdom membership alone explains a substantial amount of deviance (13.1%), a value that decreases to 2.9% when kingdoms are combined into three broad longitudinal bands (Americas, Europe–Africa, Asia–Australia) to minimize environmental collinearity.

We proceed to select the best single predictor variable or interaction term from each category to construct a combined multipredictor model. Consisting of six explanatory variables (AREA, PET, WETDAYS, TOPOVEG, STRUCT, and KINGDOM), the combined model explains 65.9% of the observed deviance in a GLM framework ( $AIC = -353.5$ ) and 70.2% in spatial linear model (SLM) ( $AIC = -456.9$ ) (Fig. 2 and SI Fig. 4). The SLM approach successfully removes spatial autocorre-

**Table 2. Global model of plant diversity**

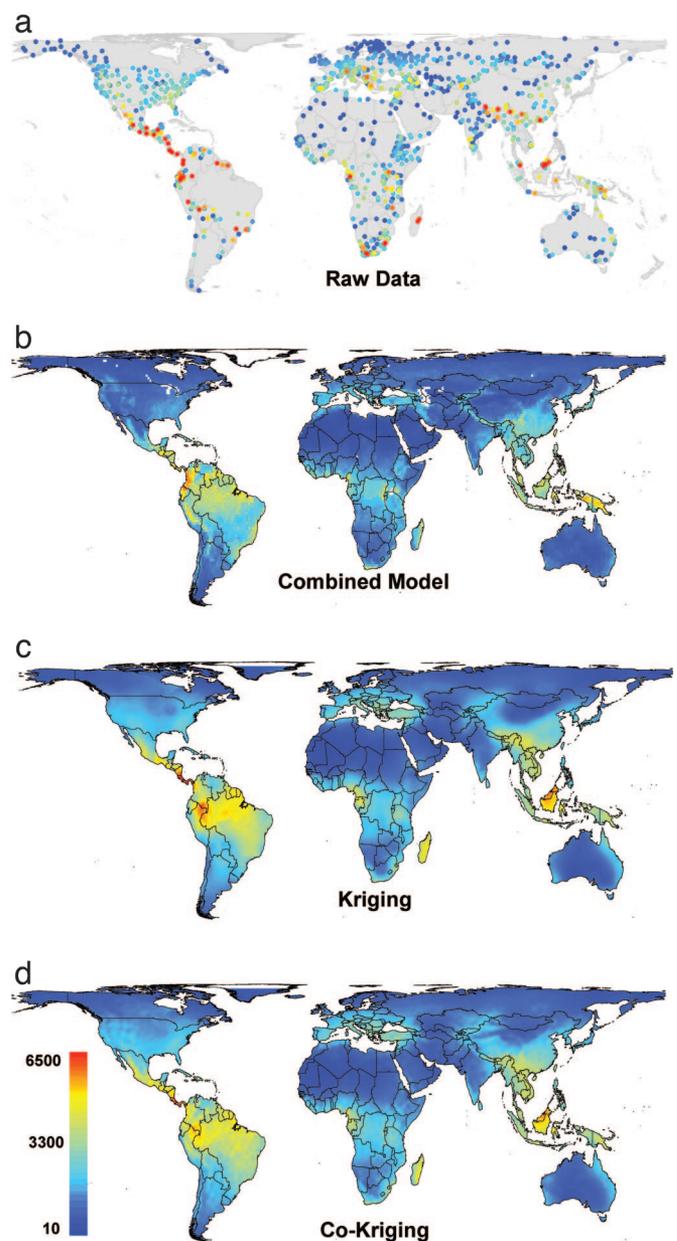
Combined model	GLM		SLM	
	Coefficient	<i>t</i>	Coefficient	<i>z</i>
AREA	0.096	9.4	0.118	11.5***
PET	0.759	18.2	0.747	12.4***
WETDAYS	0.507	14.9	0.542	12.3***
TOPOVEG	0.011	14.9	0.010	11.3***
STRUCT	0.030	5.9	0.022	4.5***
KINGDOM	—	—	—	—
NEA	−0.154	−2.2	−0.081	−1.7
AUS	−0.061	−3.9	−0.162	−2.2*
CAP	0.285	6.1	0.281	4.1***
PAT	−0.051	−2.3	−0.062	−1.5
PAA	−0.006	−0.2	−0.023	−0.5
Deviance, %	65.9		70.2	
AIC	−353.5		−456.9	
Moran's I	0.17***		−0.01NS	

Results of GLM and SLM of a combined six-predictor model. KINGDOM: NEA, Nearctic; AUS, Australis; CAP, Capensis; PAT, Palearctic; PAA, Palaeartic. Estimates for KINGDOM refer to deviations from Neotropic (NET). NS, not significant; \*\*\*,  $P < 0.001$ .

lation from the model residuals (SI Fig. 5; for a map of GLM and SLM residuals, see SI Fig. 6). No interaction terms (including the previously asserted energy–water interactions) significantly improve the model fit. The most important model predictor is PET (11.1% partial deviance; Fig. 2) followed by number of wet days and environmental heterogeneity (both 7.2%).

When controlling for environmental dissimilarities in the combined model, floristic kingdom only has a small, yet significant, effect on richness [combined model (Table 2) compared with a model without term for kingdom:  $\Delta AIC = 68$  and 2.7% deviance, GLM;  $\Delta AIC = 29$  and 0.9% deviance, SLM]. Despite above and beyond differences due to environment, the world's floristic kingdoms appear to be remarkably similar in richness. There is one glaring exception: the Southern African Cape region, highlighted before for its unique biota and apparent high richness (16, 44) but never evaluated in the global context. We find that translated into species numbers, the Cape flora has more than twice as many species (on average 655 species per  $\approx 12,100$  km<sup>2</sup> grid cell more; maximum: 1,637) per unit area than expected given its contemporary environment and topography, confirming, from a global perspective, its outstanding richness (44). The potential causes of the unique plant diversity of the Cape region are still debated and include climatic shifts from summer to winter rains starting in the Oligocene, pollinator specialization, mesoscale habitat specialization, and fire regimes, giving rise to an enormous diversification in some clades (45, 45). Crucially, we find that many regional differences in species richness that have classically been attributed to historical factors can also be predicted by contemporary differences in the environment. For instance, the long recognized greater diversity of Neotropical rainforests in relation to their African counterparts (mean  $\pm$  95% confidence interval; number of species per 12,100 km<sup>2</sup>: 2,479  $\pm$  39 vs. 1,886  $\pm$  43) can at least statistically be predicted by environmental differences alone (e.g., mean annual precipitation: 2,186  $\pm$  49 vs. 1,661  $\pm$  57 mm; mean wet days: 199  $\pm$  3 vs. 133  $\pm$  3).

In summary, our combined model successfully explains the latitudinal gradient of plant species richness (SI Fig. 4), and the predicted global map (Fig. 3*b*) confirms many regional trends and hotspots anticipated before (11, 13, 14, 16, 17, 46). Geostatistical models (Fig. 3*c* and *d*) additionally incorporate information of environmental covariation and neighborhood effects. Given the importance of these effects asserted in the SLM, they



**Fig. 3.** Global patterns of vascular plant species richness. (a) The geographic distribution of the richness data of vascular plants for the 1,032 geographic regions analyzed in this study (each dot presents the mass centroid of a geographic entity; note that regions differ in size and that species counts have not been standardized). (b–d) The species-richness maps show area-standardized predictions of three different global models across an equal area grid ( $\approx 12,100$  km<sup>2</sup>,  $\approx 1^\circ$  latitude  $\times$   $1^\circ$  longitude near the equator) based on the combined multipredictor model (b), ordinary kriging of species richness (where species richness is interpolated purely as a function of spatial autocorrelation in the response variable) (c), and ordinary cokriging (which incorporates both the spatial autocorrelation in species richness and the combined model as an underlying trend) (d).

improve the quality of predictions, especially in relatively well sampled regions (e.g., North America, Europe, and Mesoamerica).

We have shown that relatively few variables, namely a combination of high annual energy input with constant water supply and extraordinarily high spatiotopographic complexity, are able to accurately predict the location of global centers of plant richness (Costa Rica–Chocó, Tropical Eastern Andes, Atlantic



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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