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# DETERMINANTS AND PREDICTION OF BROAD-SCALE PLANT RICHNESS ACROSS THE WESTERN NEOTROPICS<sup>1</sup>

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## ABSTRACT

Patterns of broad-scale plant species richness are thought to be largely determined by (1) variation in energy and water availability among sampling units (species energy hypothesis), (2) habitat and topographic heterogeneity within sampling units (spatial heterogeneity hypothesis), and (3) regional differences in geographic configuration and history (regional effects hypothesis). However, lack of taxonomic and distribution data, particularly for tropical regions, has impeded assessments of the relative importance of these three hypotheses. We used a large botanical database to estimate the pattern of relative vascular plant richness across the western Neotropics and regression models to measure the extent to which this estimated pattern supported predictions from each of the above three hypotheses. Variation in plant richness across three major paleophysiographic regions (northwest South America, southern Central America, and northern Central America) was primarily predicted by the spatial heterogeneity hypothesis, with secondary contributions from the species energy hypothesis and, to a lesser extent, the regional effects hypothesis. Regression models that incorporated the relative contributions of all three hypotheses predicted peaks of relative species richness mostly in topographically complex areas (e.g., Sierra Madre de Chiapas, Cordillera de Tilarán, Cordillera de Talamanca, Panama's Cordillera Central, the Andes, and the Venezuelan Guayana); relatively low richness in central Mexico and Yucatán, Los Llanos of Venezuela, and in the Gran Chaco region of Bolivia, Paraguay, and Argentina; and a richness trough in lowland Amazonia relative to southern Central America, the Andes, and the Venezuelan Guayana. We discussed the contrast between our results and previous assessments that found plant richness to be primarily determined by the species energy hypothesis and predicted different patterns of plant richness across the western Neotropics.

**Key words:** Broad-scale species richness, Neotropics, regional effects, spatial heterogeneity, species energy, vascular plants.

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Patterns of spatial variation in the number of species co-occurring within broad geographic areas were discussed by naturalists of the 18th and 19th centuries (von Humboldt, 1808; Darwin, 1862; Wallace, 1878; see Hawkins, 2001), and more rigorous attempts to quantify these patterns began during the last century (e.g., Wulff, 1935; Simpson, 1964; see Mutke & Barthlott, 2005) along with the formulation of numerous hypotheses to explain them (Hutchinson, 1959; Pianka, 1966; Huston, 1979, 1994; Rohde, 1992; Palmer, 1994; Rosenzweig, 1995; Schemske, 2002; Willig et al., 2003). Yet, understanding what determines broad-scale spatial patterns of species richness still remains a central issue in ecology and biogeography (Gaston, 2000; Ricklefs, 2004; Pennisi, 2005). Recent work in this area has focused on a few prominent hypotheses,

notably the species energy (SE), spatial heterogeneity (SH), and regional effects (RE) hypotheses.

The SE, broadly defined, holds that gradients of energy and water availability across sampling units create and maintain species-richness patterns (Hutchinson, 1959; Pianka, 1966; Brown, 1981; O'Brien, 1993; Rosenzweig, 1995) through a variety of nonexclusive mechanisms (Hawkins et al., 2003; Currie et al., 2004; Evans et al., 2005; Clarke & Gaston, 2006) including the effects of these gradients on extinction (Wright, 1983), evolutionary rates (Rohde, 1992; Evans & Gaston, 2005), and species filtering according to physiological requirements (von Humboldt, 1808; Turner et al., 1987). The SH posits that variation in elevation and habitat within sampling units increases richness, again through various nonexclusive mechanisms, including species sorting

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among habitats (Rosenzweig, 1995) or isolated patches of similar habitats (Simpson, 1964) and the effect of spatial heterogeneity on diversification rates (Simpson, 1964; Jetz et al., 2004). The RE proposes that differences in richness between sampling units with similar environments but located in different regions (i.e., diversity anomalies) result from regional disparities in history and geographic configuration that, in turn, cause differences in the occurrence of particular lineages, time available for diversification, and rates of species production and extinction (Pianka, 1966; Latham & Ricklefs, 1993; Schluter & Ricklefs, 1993; Qian & Ricklefs, 2000).

Many ecologists seem to agree that some combination of the three hypotheses above provides the best, currently available, explanation of broad-scale spatial patterns of species richness (Rahbek & Graves, 2001; Ricklefs et al., 2004; Field et al., 2005; Kreft & Jetz, 2007). However, progress in establishing the relative importance of these hypotheses as explanations of broad-scale patterns of plant species richness has been hindered by the scarcity of taxonomically and spatially resolved data sets (Whittaker et al., 2005), particularly for tropical regions (Frodin, 2001; but see Kier et al., 2005). Thus, most studies are focused on a few relatively well-known life forms (e.g., Currie & Paquin, 1987; O'Brien, 1998; Field et al., 2005) or taxonomic groups (e.g., Bjorholm et al., 2005). Other studies are based on floras, checklists, and other literature sources that have little information on sampling effort (e.g., Kreft & Jetz, 2007). Yet, failure to account for sampling effort can alter our perception of spatial patterns of plant richness (Nelson et al., 1990; Parnell et al., 2003). Here, we expanded on previous efforts to overcome these problems (Jiménez et al., 2009) by assessing the relative importance of the SE, SH, and RE in determining broad-scale patterns of vascular plant species richness across the western Neotropics. In addition, we used results on the relative importance of different hypotheses to predict relative plant species richness in areas of the western Neotropics with poorly sampled floras.

## METHODS

To describe the spatial pattern of vascular plant species richness across the western Neotropics, we used 755,401 georeferenced herbarium specimen records from the Tropicos database (<<http://www.tropicos.org/>>, Missouri Botanical Garden), representing 48,264 plant species collected in central Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, French Guiana, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, Uruguay, and northern Argentina. We mapped these data on a

Behrmann cylindrical equal-area projection of the study area and used rarefaction (Gotelli & Colwell, 2001) to estimate relative species richness in  $100 \times 100$  km sampling units as the expected number of species in a random sample of size  $n$  from a set of  $N$  herbarium specimen records. To choose the value of  $n$  at which relative richness was measured using rarefaction, we balanced the benefits of increasing  $n$  in terms of increased precision of relative richness estimates against the corresponding costs in terms of decreased sample size (Fig. 1; Jiménez et al., 2009). We judged  $n = 500$  herbarium specimen records to be a reasonable compromise and retained 255 sampling units with at least 500 specimen records for further analysis (Fig. 2A, B).

Admittedly, rarefaction is unlikely to account for all error in estimates of relative richness due to differences in sampling effort, because the set of  $N$  herbarium specimens collected in a single sampling unit is unlikely to be a random sample from the individuals of all vascular plants occurring in that sampling unit (Jiménez et al., 2009). Therefore, our estimates of relative plant richness contain potentially large measurement errors that, nonetheless, can be reasonably subsumed in the error term of statistical models representing different hypotheses. Such measurement errors may affect the conclusions from our analysis mainly in proportion to its correlation with the explanatory variables relevant to the three hypotheses of interest (Jiménez et al., 2009). As a starting point, we assumed such correlation was negligible.

We used a set of regression models to simultaneously measure the extent to which the estimated pattern of relative plant richness across the western Neotropics (Fig. 2A) supported predictions from the SE, SH, and RE. For each regression model, we derived predictions from one or more hypotheses about the sign of regression coefficients relating explanatory variables to relative plant richness. Some regression models included higher-order terms (i.e., interaction or quadratic terms) that may account for small portions of the variation in the response variable when the range of the relevant explanatory variable is limited. Therefore, when the coefficients of higher-order terms were not statistically significant, we examined the performance of reduced models with no higher-order terms in an attempt to trade-off a tolerable bias for increased precision (Chatterjee & Hadi, 1983). In these reduced models, the predicted sign for regression coefficients may depend on the range and central tendency of explanatory variables. We derived predictions for the sign of regression coefficients in reduced models based on the range of explanatory variables in our sample (Fig. 3) and the

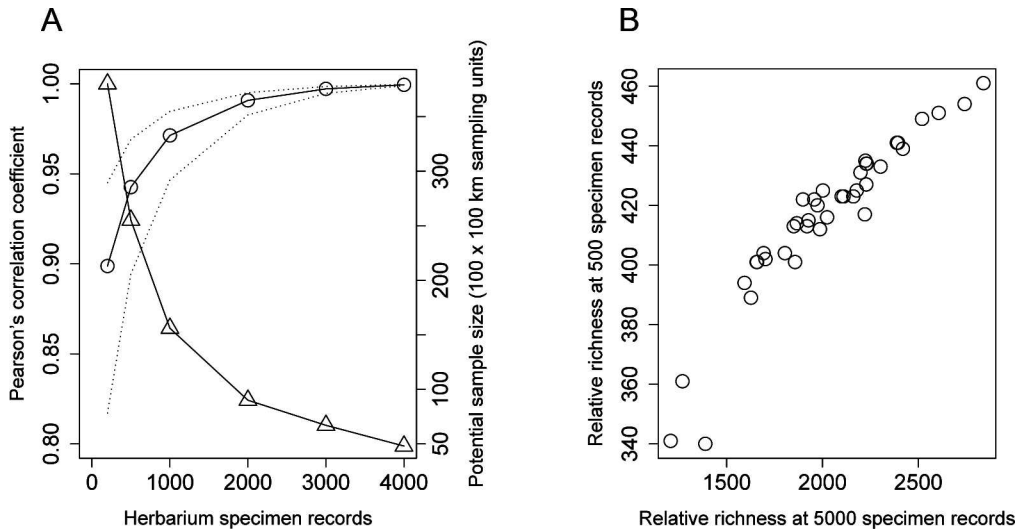


Figure 1. Trade-off between precision and sample size. —A. Pearson's correlation coefficients (line and circles) and their 95% confidence intervals (dotted lines) for the relationship between richness estimated by rarefaction as the expected number of species in 5000 specimen records and richness estimated by rarefaction at various other numbers of specimen records (in the abscissa): 4000, 3000, 2000, 1000, 500, and 200. The sample to estimate all these correlations was a set of 41 sampling units of  $100 \times 100$  km, each with at least 5000 herbarium specimen records. Also shown is the potential sample size (line and triangles): the number of sampling units in our study area that would be available for analysis if richness estimates based on rarefaction at a given number of specimen records were deemed acceptable. By deciding to estimate richness at 500 specimen records we adopted a somewhat conservative approach, trading off increases in potential sample size above 255 sampling units for relatively precise richness estimates. —B. Relationship between relative plant richness estimated by rarefaction at 5000 herbarium specimen records (in the abscissa) and 500 herbarium specimen records (in the ordinate) across 41 sampling units of  $100 \times 100$  km, each with at least 5000 specimen records.

values of regression coefficients obtained by previous studies (O'Brien, 1998; Francis & Currie, 2003; Field et al., 2005).

The SE was represented by three models thought to explain a major portion of broad-scale spatial variance in plant richness worldwide (O'Brien, 1998; Francis & Currie, 2003; Field et al., 2005; Table 1). Importantly, we selected data sources to reflect the original formulation of each model as closely as possible. Thus, for SE models 1 and 2 (Francis & Currie, 2003; Table 1) we obtained annual potential evapotranspiration and water deficit from Ahn and Tateishi (1994), while for SE model 3 (O'Brien, 1998; Field et al., 2005; Table 1) we calculated minimum monthly potential evapotranspiration using mean monthly temperature and Thornthwaite's formula (Thornthwaite, 1948; see details in Jiménez et al., 2009). We obtained data for mean annual temperature, mean monthly temperature, and annual precipitation from WorldClim (<http://www.worldclim.org/>; Hijmans et al., 2005).

The SH was represented by three regression models based on hypothesized effects on plant richness of within-sampling-unit spatial variation in elevation (Currie & Paquin, 1987; O'Brien et al., 2000; Kreft & Jetz, 2007), climate (Currie & Paquin, 1987; Linder, 2003), and soil (Linder, 2003; Tuomisto et al., 2003;

Gentry, 1988; Table 1). We calculated variance in elevation within each sampling unit from elevation data at a resolution of  $90 \times 90$  m (Shuttle Radar Topography Mission, USGS, 2004). We derived spatial variation in climate within sampling units from 19 variables measuring various aspects of temperature and precipitation at a resolution of 30 arcseconds, obtained from WorldClim. Principal component analysis on these 19 variables captured 89.4% of the total variation in the first three principal components. Because variance within sampling units in these three principal components was highly correlated (Pearson's  $r > 0.75$ ;  $P < 0.05$ ), we used only the variance within sampling units in the first principal component as an explanatory variable. We calculated variance in available water capacity and soil carbon density within each sampling unit from data at a  $5 \times 5$  min. resolution (Global Soil Data Task).

We also considered regression models that combined terms representing the SE and SH. One model was the Interim General Model second-generation (IGM2) (O'Brien et al., 2000; Field et al., 2005; Table 1), regarded as one of the best working models to explain broad-scale patterns of woody plant richness (O'Brien et al., 2000; Field et al., 2005;

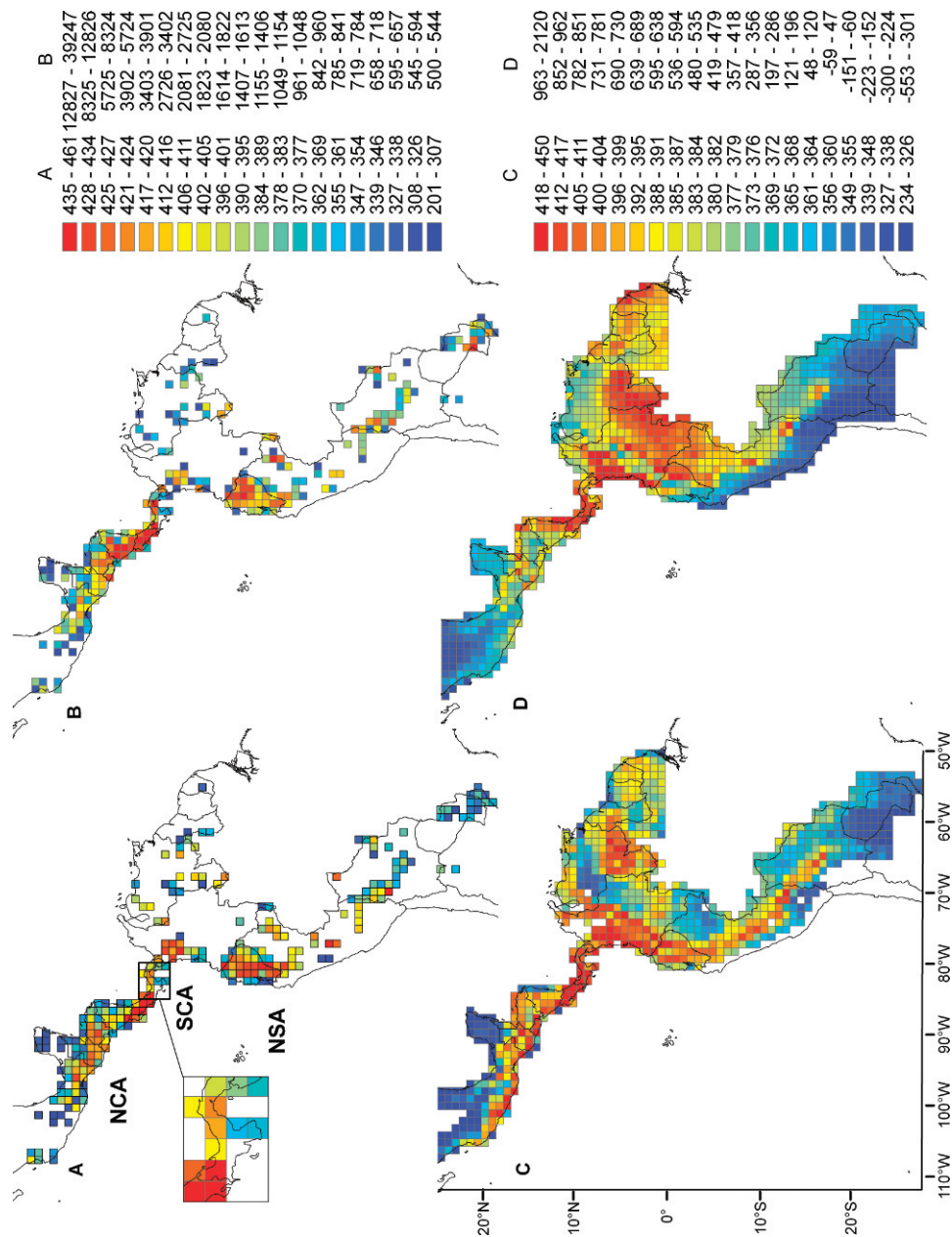


Figure 2. Relative plant richness and botanical sampling effort in 255 sampling units of  $100 \times 100$  km distributed across the western Neotropics. Each color represents an interval of five percentiles, from high (red) to low (blue). —A. Observed richness measured as the average number of species found in 1000 rarefied samples of 500 herbarium specimen records. —B. Number of herbarium specimen records. —C. Predicted relative richness based on the fit of the data in A to the nonspatial version of Interim General Model second-generation (IGM2) with regional effects (Table 2). Prediction is restricted to the sample range of explanatory variables. —D. Woody plant species richness as predicted by the global coefficients for the IGM2 (Field et al., 2005). No woody plants are predicted to occur in sampling units with negative values. NCA, N Central America; SCA, S Central America; NSA, N South America.

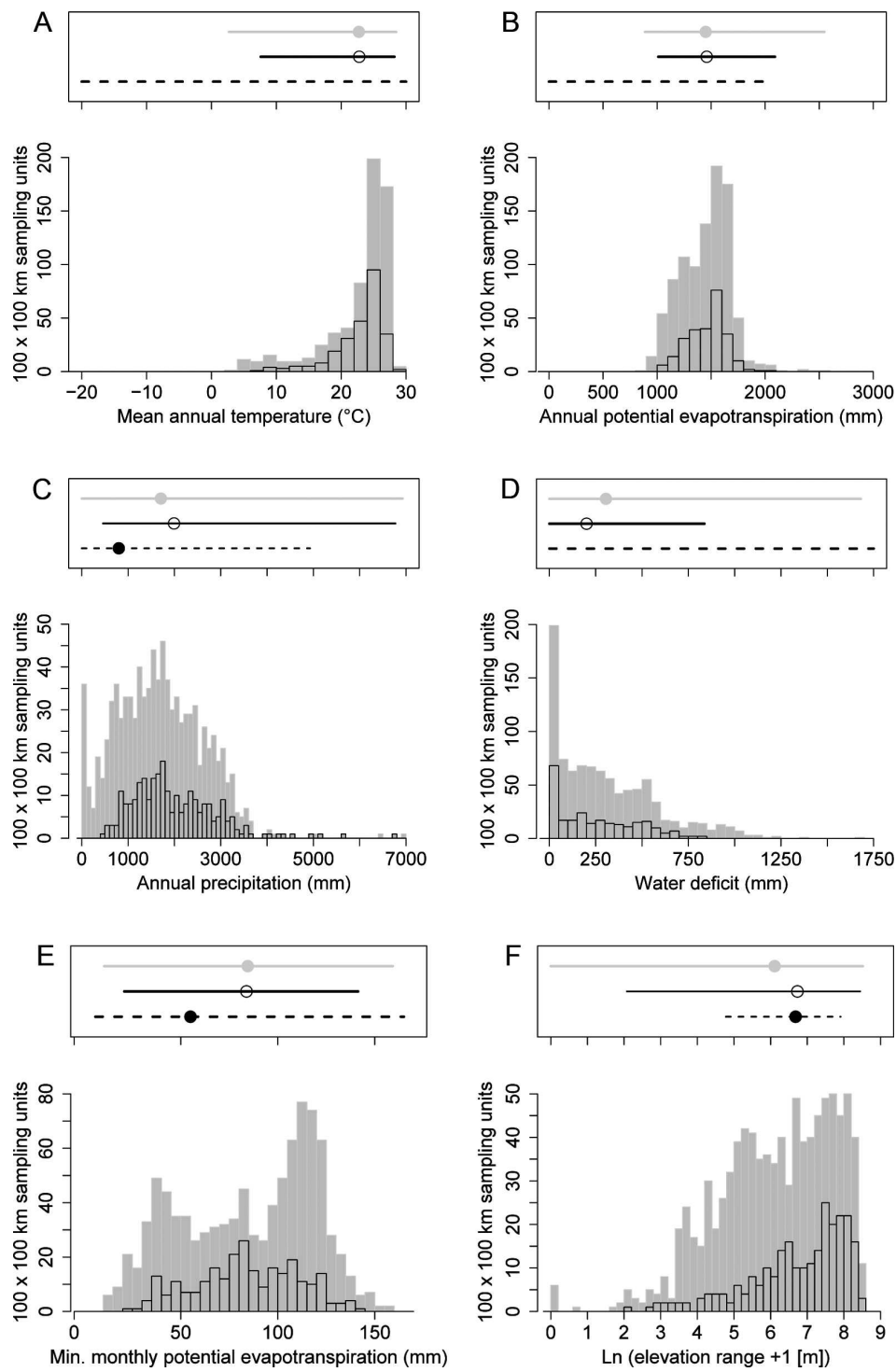


Figure 3. Distribution of explanatory variables across the western Neotropics (gray bars), and our sample of the study area (bars with black outline). At the top of each histogram, a line and a dot represent the range and mean, respectively, for the western Neotropics (gray), our sample of the study area (black), and samples used to generate species energy (SE) models and the globally specified Interim General Model second-generation (IGM2) (dashed line). The summary statistics for values of mean annual temperature (A), water deficit (D), and potential evapotranspiration (B) in the samples used to generate SE



Clarke & Gaston, 2006). While the IGM2 was specifically developed for woody plants, its conceptual basis is general and allows application to all plants, at least as an approximate representation of the SE and SH. To replicate as closely as possible the original formulation of the IGM2, we estimated elevation range for each sampling unit using the GTOPO30 arcsecond elevation data set (USGS, 2004) resampled to  $10 \times 10$  km. We constructed additional models combining terms representing the SE and SH that yielded significant ( $P < 0.05$ ) regression coefficients that were consistent with the respective predictions in all previous regression models. We examined all combinations of these explanatory variables, except when they were highly correlated. For brevity, we presented only the models with more empirical support as measured by the Akaike Information Criterion corrected (AICc) for small sample sizes, recommended when the ratio of sampling units to model parameters is less than 40 (Burnham & Anderson, 2002). Given the procedure used to construct these latter models, we refer to them as ad hoc models (Table 1).

The RE was represented by regression models that also included terms representing both the SE and SH (Table 2). This approach follows from the idea that regional effects account for variation in species richness that remains after the effect of environmental conditions of the sampling units has been accounted for (Schluter & Ricklefs, 1993). We added regional effects to regression models using dummy variables (Draper & Smith, 1998) to code intercepts and slopes for each of three major paleophysiographic regions of the Neotropics (Graham, 1997): central Mexico through northern Costa Rica (N Central America), southern Costa Rica and Panama (S Central America), and northern South America (N South America). There are at least two well-known major differences in the history of these paleophysiographic regions (Graham, 1997; Burnham & Graham, 1999): (1) N South America was isolated from N Central America for tens of millions of years, and (2) unlike N South America and N Central America, S Central America emerged from the sea just a few million years ago. In addition, the three regions were probably differentially influenced by orogenic activity, and by late Cenozoic fluctuations in climate and sea level associated with glacial advances and retreats that intensified during the Quaternary (Graham, 1997; Burnham & Graham, 1999). Following previous

approaches to examine regional effects (Schulter & Ricklefs, 1993; Ricklefs et al., 2004), we predicted differences among regions but not the direction of such differences. Variables representing the RE were removed from regression models if they did not reduce AICc values, following model simplification procedures suggested by Crawley (2002).

To confront the estimated pattern of relative plant richness across the western Neotropics (Fig. 2A) against the models representing different hypotheses, we used quantile regression through the median (Cade et al., 2005), implemented using R package *quantreg* (Koenker, 2005, 2008; R Development Core Team, 2006). We used regression through the median rather than least squares, because the response variable measures plant richness in an ordinal scale and meaningful hypotheses about variables in an ordinal scale focus on order statistics such as the median (Wolman, 2006). We gauged the extent to which the data supported different regression models examining the statistical significance of regression coefficients and their concordance with the predictions derived from the respective hypotheses. We also assessed support for different regression models using AICc. We calculated model fit in terms of  $R^1$ , the proportion of the sum of absolute deviations from the median of the response variable that is accounted for by a regression model (Cade et al., 2005).

All regression models incorporated a covariate (logarithm of area) to account for reduced area in sampling units intersecting the border of the spatial extent of the study. Pairwise correlations among predictors (Table 3) showed that no predictors included together in a single regression model were highly correlated and, thus, collinearity was unlikely to be an issue. Furthermore, collinearity due to higher-order regression terms was alleviated by mean-centering the explanatory variables of models with higher-order terms (Quinn & Keough, 2003). We tested for spatial autocorrelation in regression residuals using a permutation test for Moran's I (Fortin & Dale, 2005), implemented with R package *spdep* (Bivand, 2008). When spatial dependence in the residuals was significant, we used spatial eigenvector mapping (SEVM; Dormann et al., 2007) to construct spatial regression models that estimated the relationship between relative species richness and explanatory variables in the absence of spatial autocorrelation in regression residuals. We used a forward-selection procedure to first include in quantile regression

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← models come from Francis and Currie (2003). Summary statistics for values of annual mean precipitation (C) and minimum monthly potential evapotranspiration (E) in the samples used by Field et al. (2005) to generate the globally specified IGM2 come from O'Brien (1998), and those for elevation range (F) are from O'Brien et al. (2000).

Table 1. Results from median regression models representing the species energy (SE) and spatial heterogeneity (SH) hypotheses.

Models and variables	Pred	Regression coefficient, nonspatial	Regression coefficient, spatial
Model 1 SE, R <sup>1</sup> = 0.039 (0.212)			
Log10 area		55.34 (23.89) <sup>a</sup>	67.15 (20.26) <sup>c</sup>
Water deficit	−	−0.02 (0.02)	−0.02 (0.02)
Mean annual temperature	+	−0.13 (0.11)	−0.24 (0.07) <sup>c</sup>
Water deficit × mean annual temperature	−	2 × 10 <sup>−4</sup> (5 × 10 <sup>−4</sup> )	1 × 10 <sup>−4</sup> (3 × 10 <sup>−4</sup> )
Eigenvector 3			−119.08 (40.63) <sup>b</sup>
Eigenvector 2			210.64 (51.58) <sup>c</sup>
Eigenvector 5			−109.42 (43.95) <sup>b</sup>
Eigenvector 4			138.61 (40.18) <sup>c</sup>
Eigenvector 12			186.20 (55.10) <sup>c</sup>
Eigenvector 6			−164.99 (52.71) <sup>b</sup>
Model 1 SE reduced, R <sup>1</sup> = 0.037 (0.221)			
Log10 area		51.200 (24.81) <sup>a</sup>	44.58 (23.11)
Water deficit	−	−0.021 (0.02)	−0.02 (0.01)
Mean annual temperature	+	−0.151 (0.12)	−0.12 (0.07)
Eigenvector 2			176.65 (53.93) <sup>c</sup>
Eigenvector 3			−131.52 (40.62) <sup>c</sup>
Eigenvector 5			−98.36 (41.72) <sup>a</sup>
Eigenvector 12			193.03 (52.09) <sup>c</sup>
Eigenvector 6			−164.89 (49.37) <sup>c</sup>
Eigenvector 15			−158.76 (47.53) <sup>c</sup>
Model 2 SE, R <sup>1</sup> = 0.084 (0.177)			
Log10 area		47.80 (24.79) <sup>a</sup>	42.72 (24.06)
Water deficit	−	−0.01 (0.02)	−0.002 (0.01)
Annual potential evapotranspiration	+	0.05 (0.02) <sup>b</sup>	0.05 (0.02) <sup>a</sup>
Annual potential evapotranspiration <sup>2</sup>	−	−3 × 10 <sup>−4</sup> (8 × 10 <sup>−4</sup> ) <sup>c</sup>	−3 × 10 <sup>−4</sup> (3 × 10 <sup>−4</sup> ) <sup>b</sup>
Eigenvector 2			194.63 (49.93) <sup>c</sup>
Eigenvector 12			219.29 (52.03) <sup>c</sup>
Eigenvector 1			7.78 (51.64)
Eigenvector 3			−93.58 (44.48) <sup>a</sup>
Model 3 SE, R <sup>1</sup> = 0.109 (0.200)			
Log10 area		63.52 (12.68) <sup>c</sup>	42.15 (17.37) <sup>a</sup>
Annual precipitation	+	0.01 (2 × 10 <sup>−3</sup> ) <sup>c</sup>	0.01 (0.003) <sup>a</sup>
Min. monthly potential evapotranspiration	+	0.15 (0.13)	0.04 (0.15)
Min. monthly potential evapotranspiration <sup>2</sup>	−	−0.01 (3 × 10 <sup>−3</sup> ) <sup>b</sup>	−0.02 (0.01) <sup>c</sup>
Eigenvector 2			164.31 (47.71) <sup>b</sup>
Eigenvector 8			117.62 (51.81) <sup>a</sup>
Eigenvector 12			234.95 (57.95) <sup>c</sup>
Model 1 SH, R <sup>1</sup> = 0.143 (0.298)			
Log10 area		42.59 (15.44) <sup>b</sup>	37.97 (10.86) <sup>c</sup>
Log10 variance in elevation	+	16.477 (2.4) <sup>c</sup>	19.84 (2.11) <sup>c</sup>
Eigenvector 2			158.58 (29.35) <sup>c</sup>
Eigenvector 3			−139.58 (27.87) <sup>c</sup>
Eigenvector 12			125.16 (45.66) <sup>b</sup>
Eigenvector 11			100.16 (33.61) <sup>b</sup>
Eigenvector 10			−137.96 (33.53) <sup>c</sup>
Model 2 SH, R <sup>1</sup> = 0.132 (0.253)			
Log10 area		44.80 (24.91)	33.88 (22.81)
Log10 variance in climate PC 1	+	66.718 (6.37) <sup>c</sup>	60.75 (9.49) <sup>c</sup>
Eigenvector 2			173.27 (46.80) <sup>c</sup>
Eigenvector 3			−124.51 (41.92) <sup>b</sup>

Table 1. Continued.

Models and variables	Pred	Regression coefficient, nonspatial	Regression coefficient, spatial
Eigenvector 12			147.93 (40.46) <sup>c</sup>
Eigenvector 15			101.07 (41.73) <sup>a</sup>
Model 3 SH, R <sup>1</sup> = 0.051 (0.220)			
Log10 area		74.34 (23.89) <sup>b</sup>	53.16 (17.08) <sup>b</sup>
Log10 variance in available water capacity	+	−10.21 (5.52)	−12.78 (3.89) <sup>c</sup>
Log10 variance in soil carbon density	+	20.43 (8.33) <sup>b</sup>	22.46 (6.09) <sup>c</sup>
Eigenvector 2			126.86 (44.30) <sup>b</sup>
Eigenvector 3			−102.54 (37.80) <sup>b</sup>
Eigenvector 7			121.81 (37.62) <sup>c</sup>
Eigenvector 12			278.07 (48.86) <sup>c</sup>
Eigenvector 6			−146.83 (40.59) <sup>c</sup>
IGM2, R <sup>1</sup> = 0.218 (0.274)			
Log10 area		50.79 (8.43) <sup>c</sup>	55.51 (9.93) <sup>c</sup>
Annual precipitation	+	0.011 (2 × 10 <sup>−3</sup> ) <sup>c</sup>	0.01 (0.003) <sup>c</sup>
Min. monthly potential evapotranspiration	+	0.298 (0.11) <sup>b</sup>	0.28 (0.12) <sup>a</sup>
Min. monthly potential evapotranspiration <sup>2</sup>	−	−0.003 (3 × 10 <sup>−3</sup> )	−0.01 (0.003)
Ln elevation range	+	15.037 (1.99) <sup>c</sup>	15.06 (2.01) <sup>c</sup>
Eigenvector 2			117.08 (41.17) <sup>b</sup>
Eigenvector 8			90.23 (42.97) <sup>a</sup>
Eigenvector 3			−93.55 (39.41) <sup>a</sup>
Model 1 ad hoc, R <sup>1</sup> = 0.254 (0.298)			
Log10 area		52.70 (8.83) <sup>c</sup>	59.35 (8.40) <sup>c</sup>
Annual precipitation	+	0.01 (0.002) <sup>c</sup>	0.01 (0.003) <sup>c</sup>
Min. monthly potential evapotranspiration	+	0.29 (0.10) <sup>b</sup>	0.27 (0.12) <sup>a</sup>
Min. monthly potential evapotranspiration <sup>2</sup>	−	−0.01 (0.003) <sup>a</sup>	−0.002 (0.003)
Log10 variance in elevation	+	18.77 (1.98) <sup>c</sup>	19.64 (2.49) <sup>c</sup>
Eigenvector 2			110.38 (40.88) <sup>b</sup>
Eigenvector 3			−109.42 (38.23) <sup>b</sup>
Eigenvector 8			109.61 (43.72) <sup>b</sup>
Model 2 ad hoc, R <sup>1</sup> = 0.258 (0.300)			
Log10 area		49.93 (6.29) <sup>c</sup>	64.49 (7.37) <sup>c</sup>
Annual precipitation	+	0.01 (7 × 10 <sup>−4</sup> ) <sup>c</sup>	0.01 (0.003) <sup>c</sup>
Min. monthly potential evapotranspiration	+	0.280 (0.10) <sup>b</sup>	0.25 (0.11) <sup>a</sup>
Min. monthly potential evapotranspiration <sup>2</sup>	−	−0.01 (0.002) <sup>b</sup>	−0.003 (0.003)
Log10 variance in soil carbon density	+	5.19 (3.38)	4.54 (3.59)
Log10 variance in elevation	+	18.477 (1.9) <sup>c</sup>	18.65 (2.35) <sup>c</sup>
Eigenvector 2			94.64 (38.38) <sup>b</sup>
Eigenvector 3			−98.03 (34.85) <sup>b</sup>
Eigenvector 8			102.67 (40.44) <sup>b</sup>
Model 3 ad hoc, R <sup>1</sup> = 0.254 (0.300)			
Log10 area		43.43 (10.82) <sup>c</sup>	60.95 (16.24) <sup>c</sup>
Annual precipitation	+	0.01 (0.003) <sup>c</sup>	0.01 (0.002) <sup>c</sup>
Potential evapotranspiration	+	−0.001 (0.02)	0.03 (0.02)
Potential evapotranspiration <sup>2</sup>	−	−2 × 10 <sup>−4</sup> (−2 × 10 <sup>−4</sup> ) <sup>a</sup>	−1 × 10 <sup>−4</sup> (1 × 10 <sup>−4</sup> )
Log10 variance in soil carbon density	+	8.289 (3.90) <sup>a</sup>	6.65 (4.45)
Log10 variance in elevation	+	16.025 (1.62) <sup>c</sup>	16.88 (2.07) <sup>c</sup>
Eigenvector 2			136.09 (39.45) <sup>c</sup>
Eigenvector 3			−122.15 (31.55) <sup>c</sup>
Eigenvector 8			90.70 (40.97) <sup>a</sup>
Model 4 ad hoc, R <sup>1</sup> = (0.303)			
Log10 area			47.47 (15.19) <sup>b</sup>
Potential evapotranspiration	+		0.02 (0.01)



Table 1. Continued.

Models and variables	Pred	Regression coefficient, nonspatial	Regression coefficient, spatial
Potential evapotranspiration <sup>2</sup>	—		$-2 \times 10^{-4}$ ( $2 \times 10^{-4}$ ) <sup>c</sup>
Log10 variance in elevation	+		16.19 (2.04) <sup>c</sup>
Eigenvector 2			174.42 (34.07) <sup>c</sup>

The response variable was relative plant species richness. The first column shows names of models and explanatory variables, as well as goodness of fit ( $R^1$ ) for nonspatial regression models first and for spatial models in parentheses. The column labeled “Pred” shows the predicted signs of regression coefficients according to the respective hypothesis. The next two columns show regression coefficients for nonspatial and spatial models with standard errors in parentheses and statistical significance coded as: <sup>a</sup>,  $P < 0.05$ ; <sup>b</sup>,  $P < 0.01$ ; <sup>c</sup>,  $P < 0.001$ . PC, principal component; IGM2, Interim General Model second-generation; Log10, logarithm base 10; Ln, natural logarithm.

models those spatial eigenvectors that most reduced the spatial autocorrelation in the regression residuals (see Jiménez et al., 2009). Given that the interpretation of differences between coefficients derived from spatial and nonspatial regression models remains controversial (Dorman et al., 2007), we provided results from both types of models.

To predict relative plant richness across the western Neotropics, including areas that have been only sparingly collected, we used the predicted values from the regression models best supported by the data—that is, models that yielded statistically significant regression coefficients, were consistent with the respective predictions, and had the lowest AICc values. To avoid extrapolation, we predicted richness only in sampling units that fell within the range of explanatory variables in our sample of the western Neotropics (Fig. 3).

RESULTS

NONSPATIAL MODELS

The performance of nonspatial models representing a single hypothesis indicated that the SH had more empirical support than the SE. All three models representing the SH yielded significant regression coefficients consistent with the respective predictions, while only two out of three models representing the SE did so (Table 1). The AICc values for SH models 1 and 2 were notably lower than those for other models representing a single hypothesis, differing by  $> 17$  (Fig. 4) and indicating large differences in empirical support. SH models 1 and 2 also accounted for a higher proportion of the variation in relative species richness ( $R^1 = 0.143$  and  $0.132$ , respectively) than other models (Table 1). Thus, the relative performance of SH models 1 and 2 suggested a major role for variance (within sampling units) in elevation and climate, respectively, as determinants of plant richness across the study area.

The performance of models combining terms representing the SE and SH was, with no exception, superior to that of models representing a single hypothesis. Each of these four models yielded significant regression coefficients consistent with predictions from both the SE and SH (Table 1). AICc values for the IGM2 and ad hoc models 1 to 3 were substantially smaller than those for models representing an individual hypothesis, differing by  $> 41$  (Fig. 4). In addition, the IGM2 and ad hoc models 1 to 3 accounted for more variation in relative richness ( $R^1 > 0.21$ ) than models representing a single hypothesis (Table 1). The higher performance of ad hoc models 1 to 3 compared to models representing a single hypothesis and to the IGM2 could be partly due to over-fitting, given the ad hoc procedure used to build the former models (see Methods). However, we used the IGM2 as an a priori model and, therefore, at least in this case, the higher performance of a model that combines hypotheses relative to models that represent a single hypothesis indicates the complementary nature of the SE and SH.

All models that included terms representing the RE yielded significant regression coefficients consistent with predictions from both the SE and the SH. Each of these models also yielded significant coefficients representing regional effects (Table 2), but we had no predictions about their sign (see Methods). Models representing the RE did best overall, with lower AICc values differing by  $> 7$  from models combining terms representing the SE and SH with no regional effects (Fig. 4), although respective differences in model fit were slight (Tables 1, 2). In general, the improvement in model performance accomplished by adding regional effects was smaller than that achieved by combining terms representing the SE and SH. This finding suggests that the RE, as represented in this study, does not complement the SE and SH to the same degree that the latter two hypotheses complement each other.

Nonetheless, adding regional effects to models representing the SE and SH decreased AICc values

substantially. For example, adding regional effects to the IGM2 decreased the AICc value by 23. The resulting model suggested that, after controlling for other environmental variables, relative richness was higher in S Central America than in N South America, and higher in N South America than in N Central America, across the range of minimum monthly potential evapotranspiration and annual precipitation in our sample (Fig. 5A, B). In addition, maximum plant richness was attained at higher values along the axis of minimum monthly potential evapotranspiration in N Central America than in S Central America and N South America (Fig. 5A). Relative plant richness increased faster with elevation range (within sampling units) in N Central America than in S Central America and N South America. Relative richness in sampling units with narrow elevation ranges was lower in N Central America than in S Central America and N South America, but the difference in relative richness decreased as elevation range increased (Fig. 5C). There were differences among ad hoc models in the strength and significance of regional effects, but all models revealed that N Central America, compared with S Central America and N South America, had a lower intercept and a steeper slope relating relative richness to variation in elevation within sampling units (Table 2).

#### SPATIAL MODELS

Similar to the results from nonspatial models, the performance of spatial models representing a single hypothesis indicated more empirical support for the SH than the SE. All three models representing the SH yielded significant regression coefficients consistent with the respective predictions (Table 1). However, SH model 3 also yielded a significant negative regression coefficient for variance in potential available water capacity, contrary to the respective prediction. Two of three models representing the SE, SE models 2 and 3, yielded significant regression coefficients consistent with the respective predictions, while SE model 1 yielded a significant negative regression coefficient for mean annual temperature, contrary to the respective prediction (Table 1). Among spatial models representing a single hypothesis, SH models 1 and 2 explained more variation in the response variable ( $R^1 = 0.298$  and  $0.253$ , respectively; Table 1) and had substantially lower AICc values than the rest (Fig. 4), corroborating results from nonspatial models and suggesting a primary role for variance in elevation or climate, within sampling units, as determinants of plant richness across the study region.

Each of the five spatial models combining terms representing the SE and SH yielded statistically

significant regression coefficients that were consistent with the predictions derived from both hypotheses. In no case was there a statistically significant coefficient opposite to any prediction (Table 1). These models performed better than those representing an individual hypothesis, with a notable exception: the spatial version of SH model 1, which described a positive relationship between variance in elevation within sampling units and relative plant richness, explained more variation in the response variable and had a substantially lower AICc value than the IGM2, in both metrics similar to ad hoc models 1 to 4 (Table 1; Fig. 4). This exception strengthens the previous suggestion that variance in elevation within sampling units, a variable representing the SH, was a primary determinant of plant richness across the study region. It also suggests that spatial eigenvectors accounted for variation in relative plant richness that correlated with variables representing the SE, but not for variation in relative plant richness that correlated with variables representing the SH.

All spatial models including terms representing the RE yielded statistically significant regression coefficients consistent with predictions from both the SE and SH, as well as significant coefficients representing regional effects. In only one case was there a statistically significant coefficient opposite to a prediction: ad hoc model 3 with regional effects yielded a negative coefficient for potential evapotranspiration (Table 2). Spatial models including regional effects explained only a slightly higher proportion of the variation in the response variable than models including terms representing the SE and SH only (Tables 1, 2), and their AICc values were not consistently lower than those of other models (Fig. 4). This result contrasts with the respective comparison for nonspatial models and suggests that spatial eigenvectors accounted for variation in relative plant richness that correlated with variables representing the RE. Nonetheless, a spatial model including regional effects yielded the lowest AICc (ad hoc model 2; Fig. 4) and the highest proportion of explained variation in relative species richness ( $R^1 = 0.326$ ; Table 2). This model revealed similar regional effects to those described by nonspatial models, whereby N Central America compared to other paleophysiographic regions had a lower intercept and a steeper slope relating relative richness to variance in elevation within sampling units (Table 2; Fig. 5D–F).

#### PREDICTED PLANT RICHNESS MAPS

The models best supported by the data yielded similar patterns of predicted relative species richness

Table 2. Results from median regression models combining the species energy, spatial heterogeneity, and regional effects hypotheses.

Models and variables	Pred	Regression coefficient, nonspatial	Regression coefficient, spatial
IGM2, R <sup>1</sup> = 0.263 (0.297)			
Log10 area		55.54 (13.49) <sup>c</sup>	64.749 (18.32) <sup>c</sup>
Annual precipitation	+	0.01 (0.002) <sup>c</sup>	0.01 (0.003) <sup>c</sup>
Min. monthly potential evapotranspiration	+	0.15 (0.14)	0.07 (0.13)
Min. monthly potential evapotranspiration <sup>2</sup>	−	−0.01 (0.004) <sup>b</sup>	−0.01 (0.004) <sup>b</sup>
Ln elevation range		10.39 (1.95) <sup>c</sup>	10.55 (1.91) <sup>c</sup>
NCA		−112.35 (21.65) <sup>c</sup>	−111.42 (30.07) <sup>c</sup>
SCA		23.63 (11.96) <sup>a</sup>	29.22 (9.24) <sup>b</sup>
Min. monthly potential evapotranspiration × NCA		0.87 (0.28) <sup>b</sup>	0.70 (0.35) <sup>a</sup>
Ln elevation range × NCA		16.00 (3.23) <sup>c</sup>	15.15 (4.34) <sup>c</sup>
Eigenvector 3			−140.92 (31.76) <sup>c</sup>
Eigenvector 2			74.53 (53.74)
Model 1 ad hoc, R <sup>1</sup> = 0.284 (0.308)			
Log10 area		50.87 (7.61) <sup>c</sup>	65.41 (7.34) <sup>c</sup>
Annual precipitation	+	0.01 (0.002) <sup>c</sup>	0.01 (0.002) <sup>c</sup>
Min. monthly potential evapotranspiration	+	0.14 (0.13)	0.001 (0.12)
Min. monthly potential evapotranspiration <sup>2</sup>	−	−0.01 (0.004) <sup>c</sup>	−0.01 (0.003) <sup>a</sup>
Log10 variance in elevation	+	14.73 (2.49) <sup>c</sup>	14.13 (2.18) <sup>c</sup>
NCA		−70.49 (22.79) <sup>b</sup>	−60.06 (28.04) <sup>a</sup>
SCA		59.05 (50.46)	102.91 (53.73)
Annual precipitation × SCA		0.03 (0.01) <sup>c</sup>	0.04 (0.01) <sup>b</sup>
Min. monthly potential evapotranspiration × NCA		0.72 (0.25) <sup>b</sup>	0.69 (0.25) <sup>b</sup>
Log10 variance in elevation × NCA		14.06 (4.67) <sup>b</sup>	10.95 (5.61) <sup>a</sup>
Log10 variance in elevation × SCA		−24.58 (10.52) <sup>a</sup>	−33.43 (11.63) <sup>b</sup>
Eigenvector 3			−153.32 (29.98) <sup>c</sup>
Model 2 ad hoc, R <sup>1</sup> = 0.277 (0.326)			
Log10 area		48.65 (9.44) <sup>c</sup>	50.08 (13.57) <sup>c</sup>
Annual precipitation	+	0.01 (0.002) <sup>c</sup>	0.01 (0.003) <sup>b</sup>
Min. monthly potential evapotranspiration	+	0.31 (0.11) <sup>b</sup>	0.33 (0.12) <sup>b</sup>
Min. monthly potential evapotranspiration <sup>2</sup>	−	−0.01 (0.003) <sup>b</sup>	−0.01 (0.003) <sup>a</sup>
Log10 variance in soil carbon density	+	10.15 (3.72) <sup>b</sup>	3.77 (3.40)
Log10 variance in elevation	+	15.36 (2.42) <sup>c</sup>	15.36 (2.49) <sup>c</sup>
NCA		−111.96 (30.75) <sup>c</sup>	−86.68 (36.12)
Annual precipitation × NCA		0.01 (0.01) <sup>a</sup>	2 × 10 <sup>−4</sup> (0.01)
Log10 variance in elevation × NCA		17.84 (5.40) <sup>c</sup>	17.90 (6.11) <sup>b</sup>
Eigenvector 8			98.63 (35.58) <sup>b</sup>
Eigenvector 2			149.03 (40.37) <sup>c</sup>
Eigenvector 10			−112.11 (31.40) <sup>c</sup>
Model 3 ad hoc, R <sup>1</sup> = 0.291 (0.304)			
Log10 area		48.25 (8.73) <sup>c</sup>	44.42 (11.41) <sup>c</sup>
Annual precipitation	+	0.01 (0.003) <sup>c</sup>	0.01 (0.003) <sup>c</sup>
Annual potential evapotranspiration	+	−0.04 (0.02)	−0.06 (0.02) <sup>b</sup>
Annual potential evapotranspiration <sup>2</sup>	−	−3 × 10 <sup>−4</sup> (1 × 10 <sup>−4</sup> ) <sup>c</sup>	−3 × 10 <sup>−4</sup> (1 × 10 <sup>−4</sup> ) <sup>c</sup>
Log10 variance in soil carbon density	+	10.81 (3.85) <sup>b</sup>	13.95 (4.55) <sup>b</sup>
Log10 variance in elevation	+	12.22 (1.95) <sup>c</sup>	11.24 (2.45) <sup>c</sup>
NCA		−56.45 (17.41) <sup>c</sup>	−62.95 (22.46) <sup>b</sup>
SCA		25.56 (9.52) <sup>b</sup>	26.78 (12.07) <sup>a</sup>
Annual potential evapotranspiration × NCA		0.14 (0.05) <sup>b</sup>	0.17 (0.04) <sup>c</sup>
Log10 variance in elevation × NCA		10.74 (3.59) <sup>b</sup>	12.21 (4.55) <sup>b</sup>
Eigenvector 7			97.57 (42.37) <sup>a</sup>
Model 4 ad hoc, R <sup>1</sup> = (0.272)			
Log10 area			57.32 (13.73) <sup>c</sup>

Table 2. Continued.

Models and variables	Pred	Regression coefficient, nonspatial	Regression coefficient, spatial
Annual potential evapotranspiration	+		0.02 (0.02)
Annual potential evapotranspiration <sup>2</sup>	–		$-2 \times 10^{-4}$ ( $2 \times 10^{-4}$ ) <sup>b</sup>
Log10 variance in elevation	+		15.11 (1.94) <sup>c</sup>
NCA			–17.78 (7.04) <sup>b</sup>
SCA			32.58 (7.35) <sup>c</sup>
Annual potential evapotranspiration $\times$ NCA			0.07 (0.05)
Eigenvector 3			–184.55 (35.16) <sup>c</sup>
Eigenvector 2			83.90 (33.53) <sup>b</sup>

The response variable was relative plant species richness. The first column shows names of models and explanatory variables, as well as goodness of fit ( $R^1$ ) for nonspatial regression models first and for spatial models in parentheses. The column labeled “Pred” shows the predicted signs of regression coefficients according to the respective hypothesis. The next two columns show regression coefficients for nonspatial and spatial models with standard errors in parentheses and statistical significance coded as: <sup>a</sup>,  $P < 0.05$ ; <sup>b</sup>,  $P < 0.01$ ; <sup>c</sup>,  $P < 0.001$ . IGM2, Interim General Model second-generation; Log10, logarithm base 10; Ln, natural logarithm; NCA, dummy variable for N Central America; SCA, dummy variable for S Central America.

across the western Neotropics (Figs. 2C, 6A–D). Generally, the highest species richness was predicted in topographically complex areas such as the mountains to the east of the Isthmus of Tehuantepec including the Sierra Madre de Chiapas, the mountain ranges extending from the Cordillera de Tilarán southeast along the Cordillera de Talamanca into Panama’s Cordillera Central, the Andes, and the Venezuelan Guayana. Areas predicted to have highest richness formed a longitudinally broad band in Colombia, encompassing the Chocó region and all three Andean cordilleras, and included both Andean cordilleras in Ecuador. These areas were largely restricted to the eastern Andes in Peru and Bolivia according to most models, with the exception of ad hoc model 4, which predicted high plant richness in the

western portion of the Andes in Peru (Fig. 6C), presumably because this latter model did not include any variable explicitly measuring water availability. All models predicted relatively low richness in central Mexico and Yucatán, Los Llanos of Venezuela, and in the Gran Chaco region of Bolivia, Paraguay, and Argentina. All models also predicted a species richness trough in lowland Amazonia relative to S Central America, the Andes, and the Venezuelan Guayana. These predicted patterns of relative plant richness should be seen in the light of important differences between observed and predicted richness values. Specifically, even the models best supported by the data accounted for relatively small portions of the variation in the response variable ( $R^1 = 0.258$ – $0.326$ ; Tables 1, 2).

Table 3. Pearson’s correlation coefficients among variables used in regression models representing the species energy and spatial heterogeneity hypotheses.

	Area	PET	WD	Temp	Precip	mPET	Elev	Range	Soil	Pawc	PCA1
PET	–0.352	1.000									
WD	–0.234	0.121	1.000								
Temp	–0.301	0.489	–0.155	1.000							
Precip	–0.184	0.448	–0.518	0.392	1.000						
mPET	–0.321	0.611	–0.123	0.775	0.536	1.000					
Elev	0.137	–0.070	0.282	–0.596	–0.121	–0.382	1.000				
Range	0.172	–0.061	0.261	–0.563	–0.118	–0.375	0.951	1.000			
Soil	–0.256	0.084	–0.050	–0.055	0.145	0.121	0.069	0.061	1.000		
Pawc	–0.095	0.058	0.129	–0.083	–0.013	0.060	0.055	0.033	0.545	1.000	
PCA1	0.073	0.020	0.220	–0.444	0.031	–0.261	0.838	0.799	0.161	0.112	1.000
Rich	0.166	0.149	–0.146	–0.094	0.301	0.105	0.399	0.346	0.130	–0.008	0.401

Area, log10 area; PET, potential evapotranspiration; WD, water deficit; Temp, annual mean temperature; Precip, annual precipitation; mPET, minimum monthly potential evapotranspiration; Elev, log10 variance in elevation; Range, ln elevation range; Soil, log10 variance in soil carbon density; Pawc, log10 variance in available water capacity; PCA1, log10 variance in climate’s first principal component; Rich, relative plant richness measured by rarefaction at 500 herbarium specimen records.

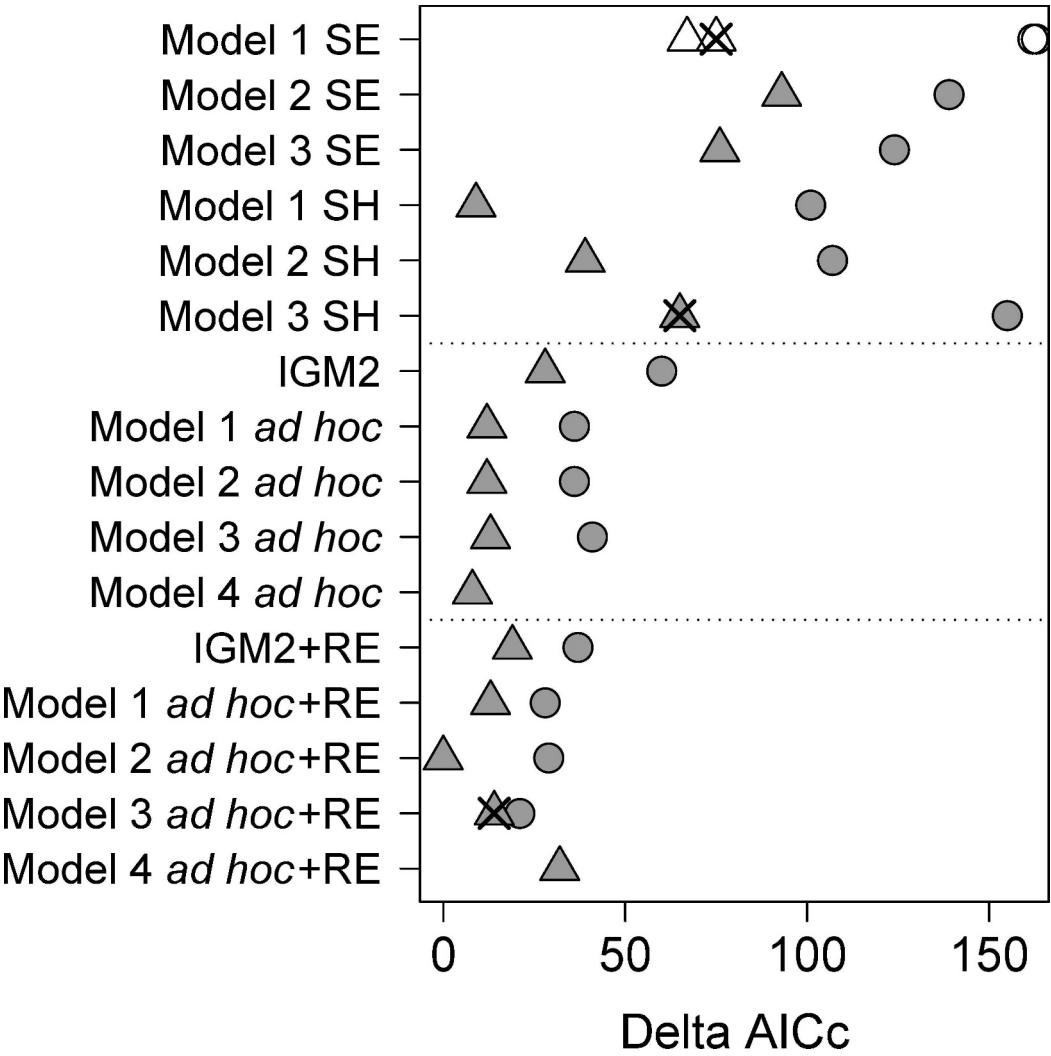


Figure 4. Support for models representing the species energy (SE), spatial heterogeneity (SH), and regional effects (RE) hypotheses estimated by differences in Akaike Information Criterion corrected (AICc) for small sample sizes (delta AICc) between each model and the model performing best (i.e., the model with the lowest AICc). The horizontal dotted lines separate models representing a single hypothesis (top), models combining terms representing the SE and SH (middle), and models combining terms representing the three hypotheses (bottom). Triangles represent spatial models and circles nonspatial models. Filled symbols represent regression models that yielded statistically significant regression coefficients consistent with the respective predictions. Open symbols represent regression models that yielded no statistically significant regression coefficients consistent with the respective predictions. Crosses mark regression models that yielded statistically significant regression coefficients that were inconsistent with the respective predictions. When higher-order terms (interaction or quadratic terms) were not statistically significant, we examined the performance of reduced models with no higher-order terms. Therefore, some models are represented by two circles or triangles.

DISCUSSION

Our results supported most a priori predictions based on previous studies about determinants of plant richness (Currie & Paquin, 1987; Gentry, 1988; O'Brien, 1998; O'Brien et al., 2000; Francis & Currie, 2003; Linder, 2003; Tuomisto et al., 2003; Field et al., 2005; Kreft & Jetz, 2007). Nine of the 13 predictions regarding the sign of regression coefficients relating

plant richness to explanatory variables were supported at least once (potential evapotranspiration and its square, minimum monthly potential evapotranspiration and its square, annual precipitation, within-sampling-unit range in elevation, within-sampling-unit variance in elevation, within-sampling-unit variance in climate, and within-sampling-unit variance in soil carbon density); three predictions were opposed once (annual mean temperature, potential evapotranspiration, and

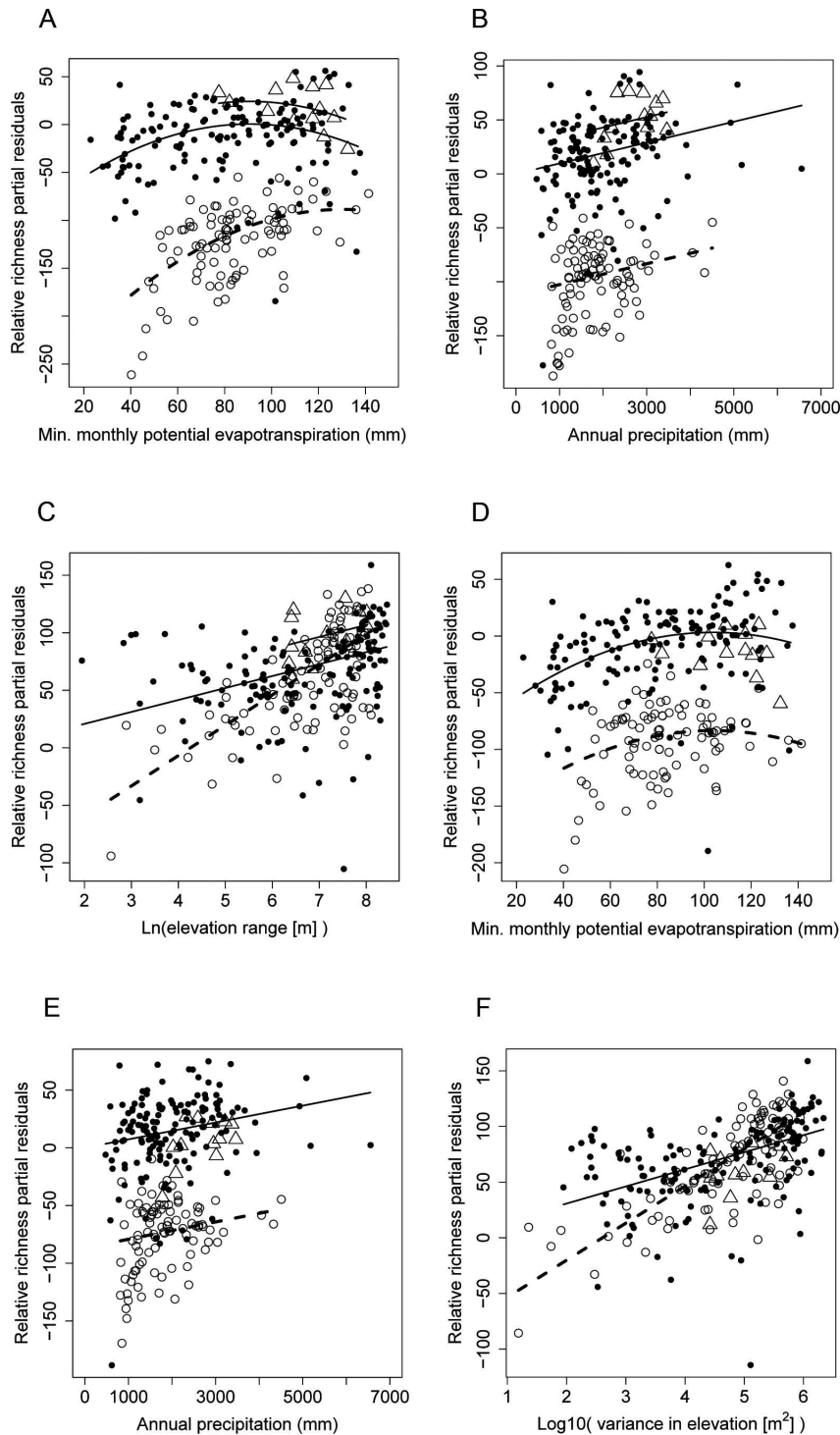


Figure 5. Plots of partial residuals (Draper & Smith, 1998) for models that incorporate the species energy (SE), spatial heterogeneity (SH), and regional effects (RE) hypotheses: —A–C. Nonspatial version of Interim General Model second-generation (IGM2) with regional effects (Table 2). —D–F. Spatial version of ad hoc model 2 with regional effects (see Table 2). These plots show the estimated relationship between relative plant richness and the variable in the abscissa when all other variables in the model are statistically controlled except for regional effects. Open circles (and dashed lines) represent N Central America, open triangles (and solid lines) represent S Central America, and filled circles (and solid lines) represent N South America.



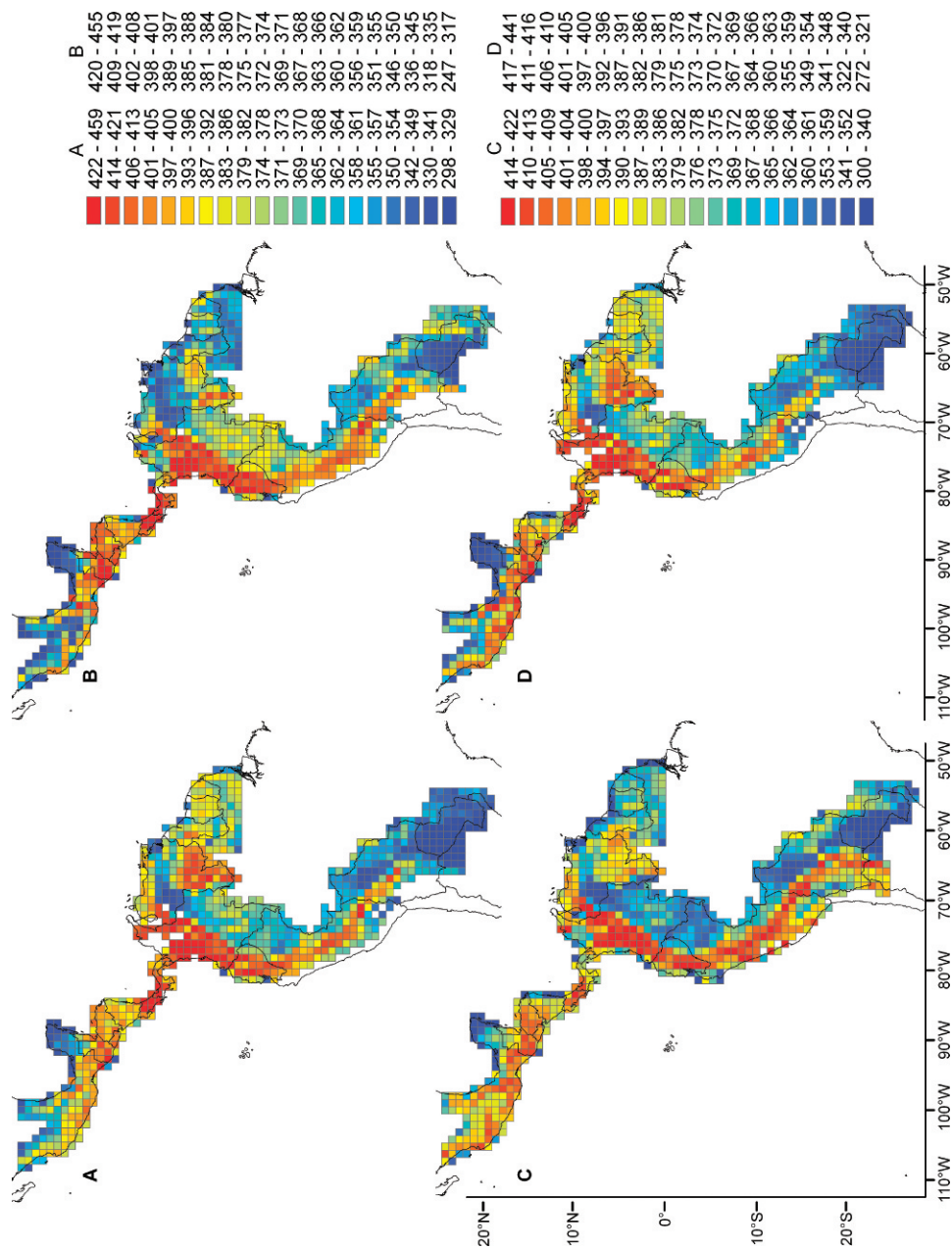


Figure 6. Predicted relative plant richness across the western Neotropics. Each color represents an interval of five percentiles of species richness measured at a resolution of  $100 \times 100$  km, from high (red) to low (blue). —A. Predicted richness based on the nonspatial version of ad hoc model 2 (Table 1). —B. Predicted richness based on the spatial version of ad hoc model 2 with regional effects (Table 2). —C. Predicted richness based on the nonspatial version of ad hoc model 4 (Table 1). —D. Predicted richness based on the spatial version of ad hoc model 4 with regional effects (Table 2). Prediction is restricted to the sample range of explanatory variables.

within-sampling-unit variance in available water capacity); and two predictions were neither supported nor opposed (water deficit and the interaction between water deficit and annual mean temperature) by statistically significant results (Tables 1, 2). We also found statistically significant differences in relative plant richness among similar environments located in different paleophysiographic regions (Table 2; Fig. 5) defined according to previous work (Graham, 1997; Burnham & Graham, 1999). These findings suggest that we used a reasonable set of hypotheses and corresponding models to examine the relative importance of the major determinants of broad-scale plant richness across the western Neotropics.

The performance of nonspatial and spatial regression models, measured by the consistency of regression coefficients with *a priori* predictions and by AICc and  $R^2$  values, indicated that explanatory variables representing the SH were the primary determinants of plant richness across the western Neotropics, with complementary contributions from variables representing the SE and, to a lesser extent, the RE. In particular, variance in elevation and variance in climate within sampling units, representing the SH, were the main predictors of the estimated pattern of relative plant richness across the study area. The models performing best overall included variance in elevation and not variance in climate, but distinguishing which of these two variables was more important was difficult because they were highly correlated (Table 3). A third variable representing the SH, variance in soil carbon density within sampling units, was included in some of the best performing models, but its role was secondary to that of variance in elevation or climate. Annual precipitation, minimum monthly potential evapotranspiration, and potential evapotranspiration, representing the SE, most effectively improved the performance of models representing the SH. Here, again, determining whether minimum monthly potential evapotranspiration or potential evapotranspiration was more important was difficult because they were correlated (Table 3). Finally, variables representing the RE sometimes increased the performance of models combining terms representing the SH and SE. Most frequent among these were variables indicating a lower intercept for N Central America than for other regions, a higher intercept for S Central America than for other regions, and higher slopes relating plant richness to spatial heterogeneity within sampling units (variance and range in elevation) and to water (annual precipitation) and energy availability (potential evapotranspiration and minimum monthly potential evapotranspiration) in N Central America than in other regions.

One of the main findings emerging from our analysis was more empirical support for the SH than

for the SE, consistent with a similar study of broad-scale plant richness across northwestern South America that found at least as much support for the SH as for the SE (Jiménez et al., 2009). This result would seem at odds with previous work indicating that variables representing the SE are more important determinants of broad-scale patterns of plant richness than those representing the SH (Currie & Paquin, 1987; O'Brien et al., 2000; Hawkins et al., 2003; Bjorholm et al., 2005; Field et al., 2005; Moser et al., 2005; Kreft et al., 2006; Kreft & Jetz, 2007). We are aware of only one earlier plant study (Pausas et al., 2003) documenting a primary role for the SH outside our study region. Below, we explore potential explanations for the differences between our results and those from previous studies, related to the characteristics of the response variable and the distribution of the explanatory variables.

Geographic patterns of plant richness measured in small sampling units (e.g.,  $\leq 1$  ha. plots) are sometimes considered broad scale (e.g., Hawkins et al., 2003), but the importance of different hypotheses can be contingent on sampling unit size. For example, the relationship between plant richness and variables representing the SE may be most evident when measured across large sampling units, while other factors may exhibit greater heterogeneity and thus be more important determinants of spatial variation in richness at smaller grains (Whittaker et al., 2001). This would seem to be at least as much of an issue for variables representing the SH. Specifically, the SH proposes that spatial heterogeneity fosters species coexistence across habitats and isolated patches of similar habitat, or that it accelerates speciation rates by increasing opportunities for isolation and ecological divergence. Both of these effects are likely increasingly opposed by dispersal as sampling unit size decreases (cf. Moser et al., 2005). Thus, the relative importance of the SH may increase with sampling unit size, as suggested by studies of bird richness (Rahbek & Graves, 2001; van Rensburg et al., 2002; Hulbert & Haskell, 2003).

Regarding procedures to estimate the response variable, previous studies estimated richness by overlapping geographic range maps (e.g., O'Brien, 1998; Francis & Currie, 2003; Bjorholm et al., 2005), while our estimates are based solely on locality data from herbarium specimens. These two methods may yield different estimates of spatial richness patterns and correspondingly different rankings of the importance of different hypotheses (Hulbert & White, 2005). Because species do not typically occur everywhere within the area delimited by range maps (Rondinini et al., 2006), richness estimates based on range maps may measure richness at a larger grain than estimates based

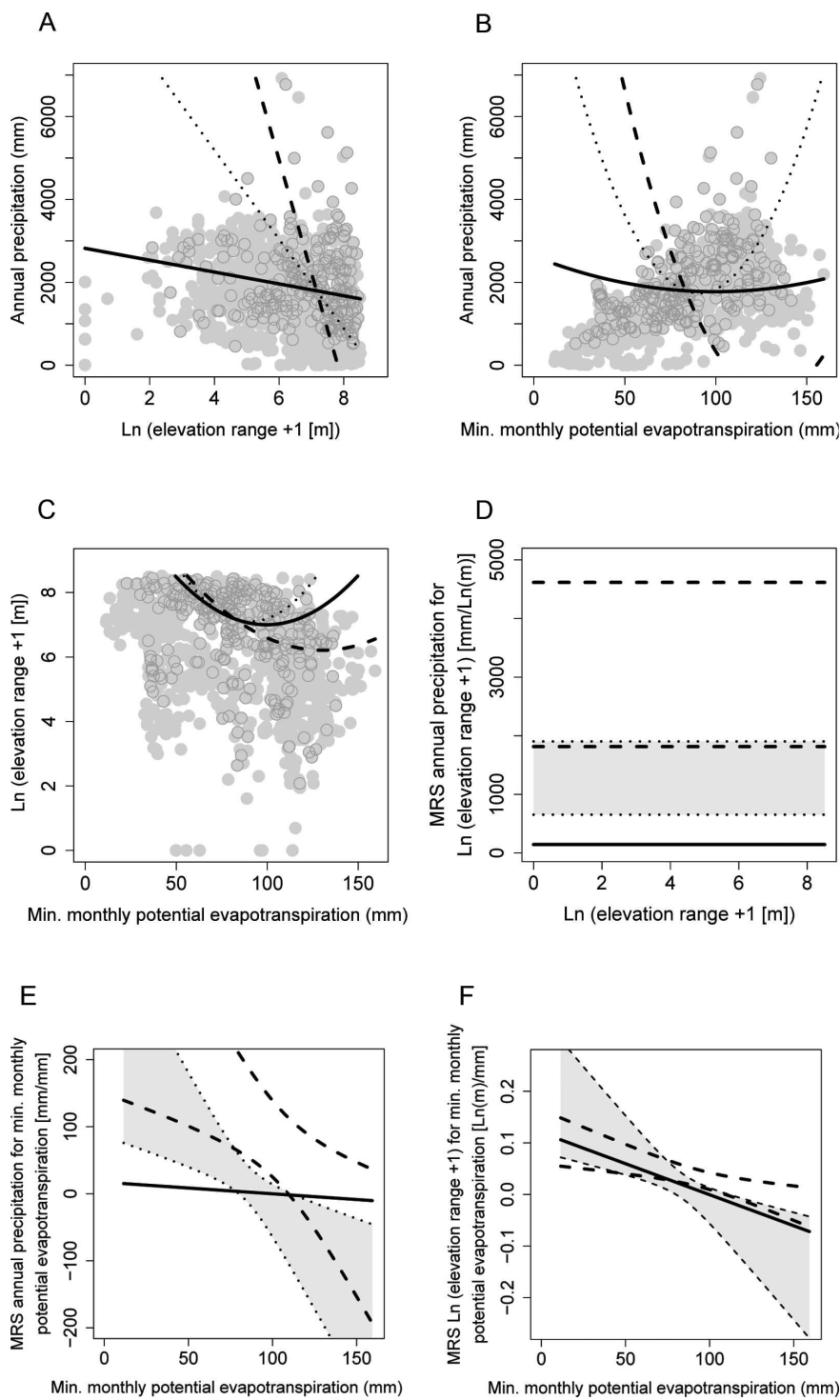


Figure 7. —A, B, C. Predicted plant richness isopleths (lines) in the bivariate distribution of (A) logarithm of elevation range and annual precipitation, (B) minimum monthly potential evapotranspiration and annual precipitation, and (C) minimum monthly potential evapotranspiration and logarithm of elevation range, across the western Neotropics (gray points), showing sampling units included in our sample (gray points with darker outline). The continuous lines are isopleths based on the global coefficients of the Interim General Model second-generation (IGM2). The dashed lines are isopleths for N Central America

on locality data (Hulbert & Jetz, 2007). As such, richness estimates based on range maps may tend to favor variables representing the SH, related to broad-scale species turnover (Hulbert & White, 2005). This expectation, however, is opposite to the difference between our results and those from previous studies.

Another important difference is that between estimates of plant richness based on floras and checklists with no correction for sampling effort (e.g., Kreft & Jetz, 2007), and our estimates based on rarefaction as an attempt to correct for spatial variation in floristic knowledge. Floras and checklists differ not only in their geographic extents, but in the quality of the data and sampling effort across these units (Frodin, 2001; Kier et al., 2005). Such heterogeneity in floristic knowledge can affect estimates of spatial patterns of plant richness and estimates of the importance of different hypotheses. We attempted to account for this heterogeneity using number of specimen records as an estimate of sampling effort (Nelson et al., 1990), assuming that the number of species found in a sampling unit is a function of the number of specimens collected in that sampling unit. Nonetheless, it is possible to imagine scenarios in which the number of specimens collected in a sampling unit is a function of the number of species occurring in that sampling unit. We think the latter is unlikely because plant species inventories of  $100 \times 100$  km sampling units across our study area are invariably incomplete. Furthermore, the inventory for each sampling unit was derived from several collecting trips that, together, are bound to obtain multiple specimens of species that are common in the sampling unit, even if some plant collectors discriminate against common species.

Studies also differ in the plant life forms on which they focus and, thus, may favor one hypothesis over another because various life forms may respond differently to different factors (Richerson & Lum, 1980; Laanisto et al., 2008). For example, tree species might be less responsive to spatial heterogeneity than nonwoody plant species (Gentry, 1982; Qian & Ricklefs, 2004). However, among studies measuring species richness of both woody and nonwoody life

forms, some conclude that the SE is more important than the SH (Francis & Currie, 2003; Moser et al., 2005; Kreft & Jetz, 2007), while others find the opposite (Pausas et al., 2003; this study). It would be useful for future studies to specifically address this issue by confronting species richness data for different life forms against models representing the SE and SH.

Differences in the central tendency of explanatory variables may also explain why our results differ from those of other studies in terms of the relative importance of the SE and SH. In tropical and subtropical regions, where energy input is high ( $> 505$  mm potential evapotranspiration, Kreft & Jetz, 2007), plant richness may be largely independent of energy and mainly determined by water availability (Hawkins et al., 2003; Whittaker et al., 2006; Kreft & Jetz, 2007) and, to a lesser extent, spatial heterogeneity (Kreft & Jetz, 2007). Despite the fact that potential evapotranspiration values were well above 505 mm in all of our sampling units (Fig. 3), we obtained statistically significant coefficients supporting predictions derived from the SE about how plant richness is related to potential evapotranspiration and minimum monthly potential evapotranspiration (Tables 1, 2; Fig. 5). Thus, our results suggest that both energy and water availability do determine plant richness across the study regions but to a lesser extent than variables representing the SH. Our sample, however, includes few sampling units from some extreme environments in the study regions, particularly those with the lowest annual precipitation ( $< 1000$  mm annual precipitation) and highest water deficit ( $> 750$  mm; Fig. 3). If the effect of annual precipitation or water deficit on plant richness decreases with increasing water availability (Gentry, 1988; Whittaker et al., 2003), our results could have underestimated the importance of water availability and, therefore, the SE.

Differences between our results and those of other studies in the relative importance of the SE and SH may relate to differences in the range of explanatory variables. Compared to studies spanning global extents (Francis & Currie, 2003; Kreft & Jetz, 2007) or aiming to develop global models (Field et al., 2005), the ranges of several variables measuring

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and the dotted lines for N South America and S Central America, according to the fit of the IGM2 with regional effects to our sample (Table 2). —D, E, F. Marginal rates of substitution (MRS) of annual precipitation for logarithm of elevation range (D), MRS of annual precipitation for minimum monthly potential evapotranspiration (E), and MRS of the logarithm of elevation range for minimum monthly potential evapotranspiration (F). The dashed lines represent 95% confidence intervals of the MRSs for N Central America and the dotted lines (and gray shading) for N South America and S Central America. These confidence intervals are based on parametric bootstrap samples (Efron & Tibshirani, 1993) of size 1,000,000, assuming a multivariate normal distribution of the regression coefficients with the variance-covariance matrix estimated from fitting the IGM2 to our sample. The continuous lines represent the MRSs based on the global coefficients of the IGM2 and have no error estimates because the variance-covariance matrix for such coefficients was not available.

energy and water availability in our sample were small (Fig. 3). Therefore, we may have underestimated the importance of the SE because the proportion of the variation in a response variable (e.g., relative plant richness) accounted for by an explanatory variable (e.g., mean annual temperature) can be a function of the sample range of the latter (Pedhazur, 1997). By the same token, in our sample, the range of a variable representing the SH, elevation range within sampling units, was similar to the sample range of a study of global extent (Kreft & Jetz, 2007) and larger than that of a study aiming to develop global models (Field et al., 2005; Fig. 3). Thus, the latter study may have underestimated the importance of the SH. If our sample is representative of the variation in energy and water availability across our study area (Fig. 3), the conclusion of more empirical support for the SH than for the SE would still be valid for this area.

We found significant regional effects among N Central America, S Central America, and N South America, consistent with studies that have explicitly tested for, and commonly found, evidence supporting the RE (Schluter & Ricklefs, 1993; Ricklefs, 2004; Kreft & Jetz, 2007). Identifying the underlying causes of differences in plant richness attributed to regional effects can be difficult, because they can actually reflect differences in environmental variables not accounted for (Schluter & Ricklefs, 1993). However, two of the most prominent regional effects that we obtained were consistent with previous assessments of historical influences on Neotropical plant diversity (Gentry, 1982). First, the lower intercept for N Central America than for other regions may be due to limited northward movement of Gondwanan clades that compose most Neotropical plant diversity in the lowlands (i.e., Amazonian-centered taxa sensu Gentry, 1982). Second, a steeper slope relating plant richness to spatial heterogeneity in N Central America than in other regions may be due to limited southward movement of Laurasian clades that are more important components of montane than lowland Neotropical floras (Gentry, 1982). Laurasian clades may then contribute more to the increase in richness associated with spatial heterogeneity in N Central America than in S Central America and N South America.

Last, we discuss implications of our findings for the perception of the spatial pattern of plant richness across the western Neotropics. Our analysis predicted peaks of relative species richness mostly in topographically complex areas (Figs. 2C, 6), consistent with a similar analysis for northwest South America (Jiménez et al., 2009) and another recent mapping effort (Kreft & Jetz, 2007: fig 3b), but contrasting with maps showing higher vascular plant richness in lowland areas than in the northern Andes (Barthlott

et al., 2005; Mutke & Barthlott, 2005; Kreft & Jetz, 2007: fig. 3c, d). The latter maps are similar to the pattern predicted by global coefficients for the IGM2 (Fig. 2D), designed for estimating broad-scale richness of woody plants worldwide (Field et al., 2005). Below, we suggest a potential explanation for the contrast between different plant richness maps of the Neotropics, based on differences between the global coefficients of the IGM2 (Fig. 2D) and the coefficients yielded by fitting the IGM2 to our sample (Fig. 2C).

The contrast between the map of predicted plant richness based on global coefficients of the IGM2 (Fig. 2D) and that based on the fit of the IGM2 to our sample (Fig. 2C) is underlain by a difference in the importance of the logarithm of elevation range relative to annual precipitation. This is illustrated by isopleths showing combinations of logarithm of elevation range and annual precipitation that, according to a given model and holding other variables constant, yield a constant predicted richness value (Fig. 7A). The slope of the isopleths based on our sample are more negative than the slope of the isopleth based on the global coefficients of the IGM2, suggesting that the importance of the logarithm of elevation range relative to annual precipitation is higher in the fit of the IGM2 to our data than in the global coefficients of the IGM2. This difference is quantified by the marginal rate of substitution (MRS; Caraco, 1979; Brown, 1988) of annual precipitation for the logarithm of elevation range, which corresponds to the negative of the slope of the isopleths in Figure 7A and measures the amount of annual precipitation needed to substitute a logarithmic unit of elevation range and maintain the same species richness in any given sampling unit (see appendix S1 note A in Jiménez et al., 2009). The MRS of annual precipitation for the logarithm of elevation range is higher in the fit of the IGM2 to our data than in the global coefficients of the IGM2 (Fig. 7D).

The foregoing contrast between the maps of predicted plant richness (Fig. 2C vs. D) also results from differences in the relative importance of minimum monthly potential evapotranspiration and annual precipitation. This can be seen in isopleths showing combinations of values of minimum monthly potential evapotranspiration and annual precipitation that, holding other variables constant, yield a constant predicted richness value (Fig. 7B). These isopleths bend because, according to the IGM2, the relationship between minimum monthly potential evapotranspiration and plant richness is quadratic (e.g., Fig. 5A). The negative of the slope of these isopleths is the MRS of annual precipitation for minimum monthly potential evapotranspiration. It measures the amount of annual precipitation needed to substitute a small increase in minimum monthly potential evapotranspiration and



maintain the same species richness in any given sampling unit. This MRS decreases as minimum monthly potential evapotranspiration increases (Fig. 7E) because, as pointed out previously, according to the IGM2 the relationship between minimum monthly potential evapotranspiration and plant richness is quadratic. As minimum monthly potential evapotranspiration increases, the decrease in the MRS of annual precipitation for minimum monthly potential evapotranspiration is steeper in the fit of the IGM2 to our data than in the global coefficients of the IGM2 (Fig. 7E). This finding suggests that the importance of minimum monthly potential evapotranspiration relative to annual precipitation is higher in the fit of the IGM2 to our sample than in the global coefficients of the IGM2.

Finally, the contrast between the map of predicted plant richness derived from global coefficients of the IGM2 (Fig. 2D) and that derived from the coefficients yielded by fitting the IGM2 to our sample (Fig. 2C) does not seem to reflect differences in the importance of the logarithm of elevation range relative to minimum monthly potential evapotranspiration. This notion is suggested by isopleths showing combinations of values of logarithm of elevation range and minimum monthly potential evapotranspiration that, holding other variables constant, yield a constant predicted richness value (Fig. 7C). These isopleths bend because the IGM2 portrays a quadratic relationship between minimum monthly potential evapotranspiration and plant richness. The negative of the slope of these isopleths is the MRS of logarithm of elevation range for minimum monthly potential evapotranspiration, and measures the elevation range (in logarithmic units) needed to substitute a small increase in minimum monthly potential evapotranspiration and maintain the same species richness in any given sampling unit. Along the axis of minimum monthly potential evapotranspiration, the MRS of logarithm of elevation range for minimum monthly potential evapotranspiration derived from the fit of the IGM2 to our data overlaps with that derived from the global coefficients of the IGM2 (Fig. 7F). This finding indicates that the importance of the logarithm of elevation range relative to minimum monthly potential evapotranspiration is similar in both cases.

The comparisons above suggest that differences among representations of plant richness across the Neotropics may result from differences in estimates of the relative importance of three main determinants of plant richness. Relative to maps showing higher vascular plant richness in lowland areas than topographically complex areas, our maps of predicted richness may assign a larger role to elevation range and minimum monthly potential evapotranspiration than to annual precipitation.

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