GLOBAL MODELS FOR PREDICTING WOODY PLANT RICHNESS FROM CLIMATE: DEVELOPMENT AND EVALUATION

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Abstract. There have been few attempts to generate global models of climate–richness relationships, and fewer still that aim to predict richness rather than fitting a model to data. One such model, grounded on theory (biological relativity to water–energy dynamics) is the interim general model (IGM1) of the climatic potential for woody plant richness. Here we present a second-generation model (IGM2), and genus and family versions of both models. IGM1 describes horizontal climate–richness relationships based on climate station data and systematic species range maps, with IGM2 additionally incorporating vertical changes in climate due to topographic relief. The IGMs are mathematical transformations of empirical relationships obtained for the southern subcontinent of Africa, whereby the re-described regression models apply to the full range of global variation in all independent climate parameters. We undertake preliminary validation of the new IGMs, first by mapping the distribution and relative spatial variation in forecasted richness (per 25 000 km²) across the continent of Africa, then by evaluating the precision of forecasted values (actual vs. predicted) for an independent study system, the woody plants of Kenya. We also compare the IGMs with a recent example of purely statistical regression models of climate–richness relationships; namely, the "global" model of A. P. Francis and D. J. Currie for angiosperm family richness. We conclude that the IGMs are globally applicable and can provide a fundamental baseline for systematically estimating differences in (woody) plant richness and for exploring the hierarchy of subordinate relationships that should also contribute to differences in realized richness (mostly at more discrete scales of analysis). Further, we found that the model of Francis and Currie is useful for predicting angiosperm richness in Africa, on a conditional basis (somewhere, sometime); we examined the relationship that it describes between climate and richness. Lastly, we found that indices of available soil water used in "water-budget" or "water-balance" analyses are not proxies for available liquid water as a function of climatological dynamics.

Key words: Africa; climate; climatic potential for richness; diversity gradients; interim general model; Kenya; model evaluation; species richness; water–energy dynamics; woody plant diversity.

INTRODUCTION

It has long been known that global gradients in richness covary with global gradients in climate. The development of statistical models of this relationship that apply globally is an important but elusive goal for ecologists. In addition to improving our understanding of diversity patterns, such models could prove useful for predicting reasonable values of plant or animal richness where actual values are unknown, and for modeling how changes in climate could alter the richness (and vegetation) patterns we see today.

Attempts to apply models, developed in particular regions, to other regions have produced some success

but have tended not to result in globally applicable models (e.g., Currie and Paquin 1987). Such work tends to focus on mid to high latitudes; regions for which data availability is better, but which contain relatively few of the world's species. An exception is an interim general model (IGM) of the "climatic potential for (woody) plant richness" (O'Brien 1998). Rather than using a purely statistical approach, O'Brien worked from first principles to develop a first-order mechanistic explanation for covariation between climate and richness globally: biological relativity to water–energy dynamics (O'Brien 1989, 1993, 1998). This idea effectively links water–energy dynamics (work done by water) to fundamental parameters of both climatological and biological dynamics, at all scales of analysis: liquid water and solar energy (e.g., hydrologic cycle and photosynthesis, respectively). In accord with energy's dynamic relationship with the state of water, the model describes the relationship of climate to woody plant

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richness as a linear function of rainfall and an optimal (parabolic) function of insolation (O'Brien 1993, 1998).

Empirically, model development was based on climate and richness data for the southern subcontinent of Africa (from 15° S to 35° S latitude) at the macro scale (25 000 km^2 grain), which spans tropical to temperate climate and vegetation. Regression analyses suggested that the best climate variables for describing ''available liquid water'' and ''optimal energy'' conditions were annual rainfall (R_{an}) and minimum monthly potential evapotranspiration (PET_{min}), respectively: species richness $\propto R_{an} + (PET_{min} - (PET_{min})^2)$. An empirically based global model of this relationship depends on the availability of qualitatively similar ''actual'' richness data with global coverage. Because of the lack of such data (see Appendix B), the southern African model (SAF1) was mathematically transformed so that it applies to the full global range of variation in R_{an} and PET_{min} (O'Brien 1998). The transformation was necessary because energy's parabolic function prevents extrapolation to climates where energy values fall outside the range sampled in southern Africa. O'Brien (1998) showed that the resulting interim general model (IGM1) of the climatic potential for richness generates reasonable estimates for woody plant species richness elsewhere in the world (United States, South America, Africa, China) in terms of both relative differences (gradients) and actual values (for the United States).

Since development of the IGM1 for species richness, we have investigated two other implications of biological relativity to water–energy dynamics: (1) the same relationship should apply over time, and (2) inclusion of vertical changes in climatological dynamics as a function of topographic relief should improve model fit. First, if water–energy dynamics are fundamental to life, the same dynamics that apply over space today, should apply over time. If so, the same climate–richness relationships applying to species should apply to genera and families. O'Brien et al. (1998) found this to be true for southern Africa; the strength of the relationship being almost identical at species and genus levels, but significantly weaker for family richness. The last is unsurprising for the following reasons (see also Qian and Ricklefs 2004). Since terrestrial life began, both climatological and biological dynamics have been subject to change due to independent geological dynamics (e.g., plate tectonics and diastrophism). These processes necessarily alter the location of land and sea relative to both the horizontal and vertical vectors of climatological dynamics. The effects are evident today in continental disjunctions and taxonomic vicariance, and in the idiosyncratic effects of topography on the prevailing climate and richness of an area (e.g., orographic rainfall and rainshadows, and ''hot spots'' and refugia, respectively). Although the horizontal vector is inherent in IGM1, the vertical vector is not. The

second implication that we tested has two parts: (1) inclusion of the vertical vector should increase the strength and precision of climate–richness relationships; and (2) given the more recent evolution of modern genera and species, the increase should be greatest with regard to family richness. On adding topographic range to the species, genus, and family models for southern Africa, the strength and precision of climate–richness relationships increased from 78.8, 79.8, and 69.7% (SAF1 models) to 85.6, 86.8, and 81.5% (SAF2 models), respectively; the greatest improvement being in family richness (O'Brien et al. 2000). Herein we present IGMs for species, genus, and family richness that were developed from these findings.

This and other evidence reviewed elsewhere (e.g., Whittaker et al. 2001, Hawkins et al. 2003) has contributed to a growing shift from a traditional emphasis only on the relationship of energy with richness, to one whereby both liquid water and energy are considered when describing climate–richness relationships. One recent example of this shift is a ''global'' statistical model of the relationship of climate with angiosperm family richness developed by Francis and Currie (2003; hereafter, F&C model). They found that their model accounts for a greater portion of the variation in family richness ($\sim$84%) than does the IGM1 when its parameters are regressed using their data ($\sim$63%). However, such a discrepancy is expected given differences in richness (woody plant vs. angiosperm families) and climate data, and especially given that IGMs are explanatory regression models, rather than simply statistical regression models. In addition to meeting more stringent statistical criteria, the IGMs had to meet theoretical and empirical criteria, with the latter taking precedence over statistical strength (R^2) when selecting the ''best'' model. As a consequence, the best explanatory model may not be the ''best-fit'' statistical model. These and other important differences mean that the IGMs describe a general climate–richness relationship (everywhere, always); by comparison, given the a priori conditional nature of its water variable, the F&C model describes a conditional one (somewhere, sometime). (See *Results: Model terms and global application.*)

Our aims are therefore twofold. First, we present the second-generation IGMs (IGM2) for species, genus, and family richness, along with the hitherto unpublished IGM1s for genus and family richness. We examine their ability (1) to estimate absolute values of woody plant richness outside of southern Africa, specifically in Kenya, and (2) to describe the relative variation in predicted richness across the continent of Africa. The predicted pattern should reflect expected or known differences in richness and vegetation. The focus on Africa is in keeping with the paucity of convincing empirical relationships between richness and energy within the tropics, where rainfall seems to dominate. Africa is also suitable for generating a global

model since virtually the full range of variation in IGM climate parameters occurs there. Secondly, we compare the IGMs with the F&C model. We illustrate the similarities, but also the difference between explanatory and purely statistical regression models of climate–richness relationships. We focus attention on theoretical and empirical discrepancies between models, rather than purely statistical ones.

For reasons of limited space, and to save duplication, we do not attempt to review relevant literature. This has burgeoned in recent years, and contains richly contrasting views of controls on diversity (notably Huston 1994, Whittaker et al. 2001, 2003, Blackburn and Gaston 2003, Hawkins et al. 2003, Colwell et al. 2004, Currie and Francis 2004, Qian and Ricklefs 2004).

Conceptual basis: biological relativity to water–energy dynamics

The following is drawn from E. M. O'Brien (*unpublished manuscript*) and briefly summarizes what is meant by biological relativity to water–energy dynamics and how it applies to terrestrial life.

Theoretically, the idea follows from first principles governing climatological, biological and ecological dynamics that can be gleaned from standard references and texts. The key is liquid water.

In terms of climatological first principles, given the Earth's energy regime, water is the only matter at the Earth's surface that is fully dynamic as a function of energy–matter exchange. Like all other matter at the Earth's surface, water is subject to changes in form and location. In addition, however, water occurs in and moves through all three states, primarily via climatological (atmospheric) dynamics—the hydrologic cycle. When this is combined with water's physical properties, the resulting water–energy dynamics (work done by water) account for almost all work done at the planet's surface throughout geological time. In terms of terrestrial life, climatological water–energy dynamics determine the very existence of water on landmasses, as well as its state, amount, duration and, in conjunction with topography, its distribution.

In terms of biological first principles, liquid water is the essential matter and matrix of life (see details in Franks 2000). Its physical properties make it the key agent of biological dynamics, driving all biological processes and functions, everywhere and always. Since the state of water varies as a function of ambient energy conditions, this a priori means that biological dynamics are restricted to optimal energy conditions—the range in which water is liquid and energy (light/heat) is still available for work. Outside this envelope biological dynamics cease (plant dormancy, aestivation, hibernation, death, etc.). Within this range the capacity for biological dynamics should vary as a function of both energy

and water availability, reaching maximum capacity where surface water from precipitation remains in a liquid state year-round and its amount exceeds the climatological demand (evaporation).

In terms of ecological first principles, the direct and primary relationship between climate and terrestrial life should be its relationship with plants, whereby raw energy, water and essential abiotic matter are transformed into biotic energy and matter. There should be a strong secondary relationship between climate and animal richness, via trophic plant–animal exchange, as found by Andrews and O'Brien (2000) for the distribution and richness of mammals in southern Africa. Finally, climatological dynamics are independent of life. Although secondary and tertiary feedbacks develop if life exists (e.g., vegetation cover decreasing albedo), life per se is not necessary to the operation of climatological dynamics. Crucially, however, climatological dynamics are necessary for terrestrial biological dynamics. Thus realized climate limits the capacity for terrestrial biological dynamics—and over time we expect richness to respond to this.

Other independent and dynamic parameters (e.g., geomorphological water–energy dynamics) also limit the capacity for biological dynamics (e.g., via dissolved nutrients), and must form part of a complete explanation for spatial richness patterns. However, given both the smaller distances over which these parameters exhibit measurable heterogeneity and their dependence on climatological water–energy dynamics, their inclusion must await the development of trans-scalar modelling (O'Brien 1989, O'Brien et al. 2000, Whittaker et al. 2001). In the interim the IGMs describe only the first-order "climatic potential for richness" and assume all else to be equal or non-limiting.

MATERIALS AND METHODS

The thrust of regression analysis can be explanation or simply statistical description. In either case, relationships need to be empirically plausible and based on analyses carried out at an appropriate scale (grain size). Sampling area should be held constant. If globally applicable predictive models are a goal, then the sampled variation in independent model parameters should be representative of (or reasonably extrapolated to represent) their full range of variation globally, and spatial autocorrelation in richness values should be minimized, if not eliminated, to avoid biasing model development, a priori, towards particular richness and associated climate conditions. Unlike purely statistical models, explanatory models explicitly test potential explanations for phenomena rather than simply documenting their existence. They should be both empirically and theoretically plausible in terms of how explanatory variables relate to each other and to the response variable. Correlation between explanatory
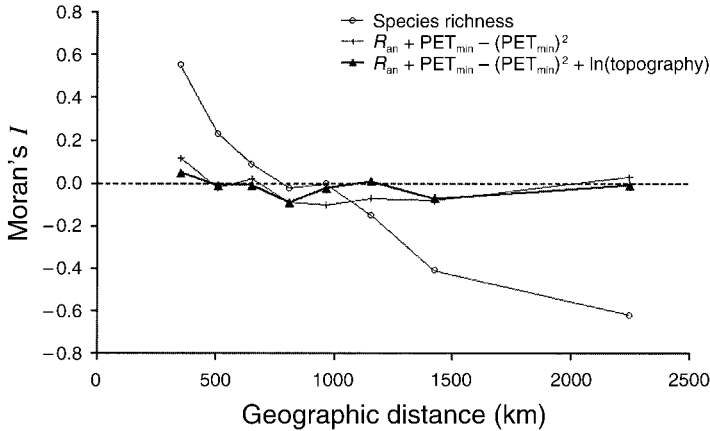
FIG. 1. Spatial correlograms for the southern African (SAF) data used in Interim General Model (IGM) development ($N = 65$ grid cells, each 25 000 km²): woody plant species richness; SAF1 residuals (rainfall [R_{an}] + PET model); and SAF2 residuals (rainfall + PET + topography model). The species richness correlogram is significant ($P < 0.001$, Bonferroni approximation), with the two smallest and two largest distance classes being significant at $P < 0.05$ after Bonferroni correction. The SAF1 correlogram is significant ($P = 0.011$), but the only significant point on this is the smallest distance class. The SAF2 correlogram is not significant ($P = 0.597$).

variables should be minimized to avoid (1) misleading (inflated) R^2 values resulting from redundancy, and (2) the problem of unstable parameter estimates, which can obscure the role of important ''missing'' environmental variables. Thereafter, selection of the ''best'' explanatory models should be based on theoretical criteria (plausibility, generality, simplicity, parsimony) and lastly on statistical strength.

Development of second-generation Interim General Models (IGM2s)

All of the southern African models (SAFs) and IGMs are explanatory regression models. Empirically they describe with minimal redundancy how water–energy dynamics relate to both climatological and biological dynamics. The capacity for atmospheric water–energy dynamics and biological water–energy dynamics (e.g., photosynthesis) should tend to increase with insolation (and evaporation off oceans), but only as long as available liquid water meets or exceeds the atmospheric energy demand for water and evapotranspiration off of landmasses. Theoretically the models describe one fundamental outcome of biological relativity to water–energy dynamics; that is, the relative capacity for changes in the form (richness) or location (distribution) of terrestrial life, over space and time.

Multicollinearity was minimized, first by restricting models to one water variable and one energy variable, both of which had to be dynamic first-order climatological parameters. Secondly, the energy and water variables used are as weakly correlated as possible ($r \approx$ 0.5 in southern Africa, and in Africa in general), and empirically they are temporally independent of each other. The minimum monthly amount of potential evapotranspiration (PET$_{min}$) usually occurs in winter, when rainfall tends to be least. This is consistent with most seasonal changes in climate globally. The topography variable, ln(topographic range), models the potential effects on richness of vertical variation in climate, such as environmental and adiabatic lapse rates. It is weakly correlated with the other explanatory variables ($r = 0.409$ and $r = -0.032$ [not significant] with

R_{an} and PET$_{min}$, respectively, in southern Africa). Note that the natural logarithm of topographic range is only slightly better statistically than a linear function; but it is more reasonable than the simpler linear function because of the increase in surface area (and habitats) that can be occupied as topographic relief increases (O'Brien et al. 2000).

The potential effects of spatial autocorrelation were first reduced by using only richness samples associated with climate stations (SAF1), and then eliminated by the addition of the topography variable, as indicated by the spatial distribution of residuals for SAF1 (O'Brien et al. 2000). No spatial autocorrelation remains in the residuals of SAF2 (Fig. 1).

Finally, we argue that the intercept should be negative, both theoretically and empirically. A negative intercept indicates that the relationship originates from the explanatory variables. Richness should be zero in the absence of liquid water, even when energy conditions are optimal (e.g., Peruvian coastal desert), since no life can exist without liquid water. Positive intercepts can be taken to indicate deficiency of the model, such as a missing variable. Negative predicted values should be treated as predictions of zero taxa. They can be taken to indicate the degree of increase in water and/ or energy needed before any richness is expected (e.g., Antarctica).

Mathematical transformation of the best southern-African models (SAF1 for genus and family; SAF2 for species, genus, and family) into IGMs followed exactly the same methods as those detailed in O'Brien (1998), except that topographic range was included in IGM2s (see Appendix B). For the mathematical transformation to be reasonable, there should be strong correlation ($r > 0.7$ and ideally $r > 0.9$) between forecasted richness values generated using the three empirical SAF models and those generated using IGMs, with minimal change in the unexplained variance. This was the case for IGM1 for species richness: $r \approx 0.97$ (O'Brien 1998). Thus it is reasonable to assume that the strength (R^2) and associated error term (RMSE) of the relationship of
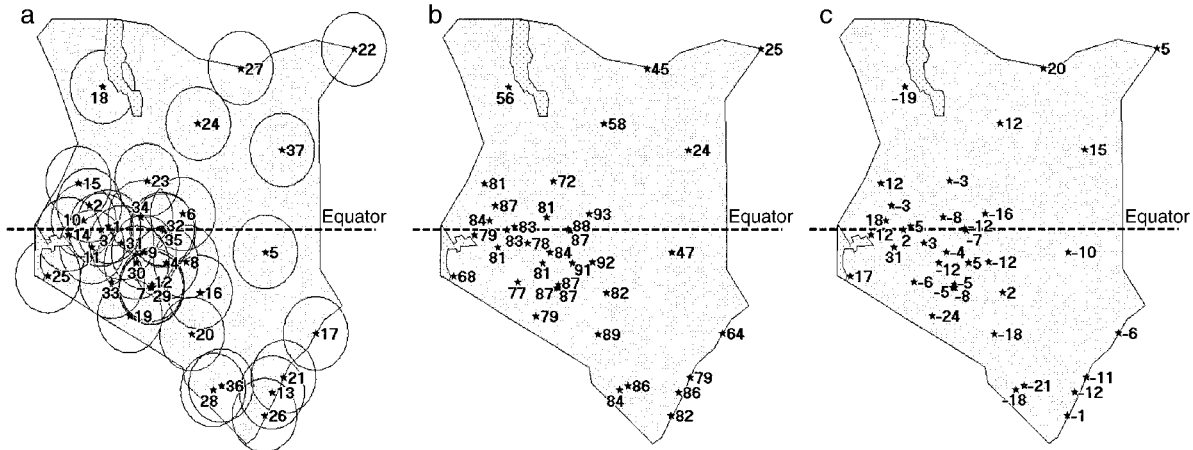
FIG. 2. Maps of Kenya showing: (a) the locations and identification numbers of the climate stations and the 25 000-km² circles surrounding them; (b) woody plant family richness per circle; and (c) "residuals" from IGM2 family level (i.e., forecast minus observed family richness). Large lakes (Turkana and Victoria) are indicated (stippled fill). Circles that have <80% of their area as land in Kenya, although shown here, are excluded from consideration in the paper; these are numbers 13, 17, 19, 21, 22, 25, 26, 27, and 28.

climate with richness in southern Africa also apply with respect to IGMs. As demonstrated for species richness by O'Brien (1998), this assumption is supported mathematically if there is little difference between the ideal SAF model (based on PET_{min}) and the corresponding IGM in terms of the coefficients for annual rainfall and, in the case of IGM2, topographic relief. (Compare ideal SAF models in O'Brien et al. [1998] with IGMs reported here.) Given the increased range in PET_{min} values, IGM coefficients for PET_{min} should markedly decrease relative to ideal SAF model coefficients. And, given the greater range of positive (potential) richness values, the intercept value should increase but remain negative.

African climate and topography data

We used Thornthwaite and Mather (1962–1965) for climate data from 980 stations in Africa (i.e., mean annual rainfall and potential evapotranspiration, both of which are dynamic climate variables). Thornthwaite's PET is a proxy for the intensity of insolation at the Earth's surface. It measures the energy demand for liquid water (mm), and thus the role of energy in climatological dynamics (evaporation and transpiration). The data were calculated using a formula he derived from experimental data on the amount of water evaporated and transpired from samples of grass-covered land never suffering from lack of water. The formula requires data on prevailing temperature and intensity of insolation at a given time (date) and place (latitude). Unlike many measures of PET, his is not adjusted to sea level and thus measures the energy (heat/light) regime actually influencing vegetation at the Earth's surface.

Following O'Brien et al. (2000), topography data were extracted from the USGS DEM of Africa, and resampled to 0.1° resolution, giving >200 elevation points/25 000-km² grid cell. The minimum value was subtracted from the maximum to give the "topographic range" (in meters), for each grid cell. Values were assigned to the 980 climate stations according to the grid cell that they occupied

Examination of the spatial pattern of model predictions

All IGMs were used to predict the climatic potential for richness across the continent of Africa, based on data from the 980 climate stations. The same was done for the F&C model at the family level (using the Thornthwaite climate data). Examination of the resulting patterns in forecasted richness, and how they relate to variation in vegetation and physiography, was undertaken following O'Brien (1998).

Actual vs. predicted richness for Kenya

All the IGMs forecast richness for a circular area of 25 000 km² (i.e., within a radius of 90 km of a climate station), the same area as the grid cells used in model development (e.g., O'Brien 1993). Actual woody plant richness data for Kenya were calculated accordingly, based on presence–absence data per circle, with each circle centered over a climate station (Fig. 2). Presence–absence data were obtained using a comprehensive set of distribution maps and site location data for Kenyan woody plants (Beentje 1994). Following the same criteria as in O'Brien (1993) to determine which species to include, 1417 out of 1862 species were retained; these represented the largest and longest lived of plant species, and thus those most likely to be robust indicators of climate conditions. Those eliminated were non-native species, plants ≤2.5 m in height, and/or plants that are not truly woody. The distributional rang-

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es of higher taxa were determined by aggregating ranges of species within genera (635 genera in total), and within families (126 families).

Distribution maps from Beentje (1994) consist of presence/absence data per pixel, with pixel resolution of half a degree (30′). Given that Kenya lies on the equator, the spatial resolution of the distribution data is ~55.5 km and pixel area is effectively constant at ~3080 km^2. Distribution information for ~30% of the species in Beentje (1994) is given only as named collecting localities. For these, all the named places were assigned latitude and longitude coordinates using various sources, including Polhill's (1988) checklist of collecting localities, Microsoft Encarta CD-ROM, and a Kenyan postal districts booklet. These locations were then rasterized into the same 30′ grid system. We calculated actual richness per circle using MapInfo Professional (MapInfo, Windsor, Berkshire, UK) by amalgamating the species data from those pixels whose centers lie within each circle. Circles with <80% of their area as land within Kenya's borders were removed from the data set, leaving a total of 28 circles (Table 2a).

We also calculated actual woody plant family richness for 34 900-km^2 circles (105-km radius) using the same protocol as for the 25 000-km^2 circles (Table 2b). This corresponds to the sampling area used by Francis and Currie (2003) for their model (see Table 1b for error terms). Of the 37 circles centered on Kenyan climate stations, 27 met the equal-area criterion at this grain size.

Woody plant family richness differs from angiosperm family richness, which includes nonwoody families and excludes gymnosperm and pteridophyte families. A comprehensive series of species range maps does not exist for Kenyan angiosperms. This prevents direct comparison between the IGMs and the F&C model, but some testable implications exist. We know there to be 245 plant families in Kenya (H. Beentje, *personal communication.*). Excluding gymnosperm (3) and pteridophyte (31) families, this leaves 211 as a maximum for angiosperm family richness in any circle. According to the Francis and Currie richness data (not all derived from range maps) the global maximum angiosperm family richness in 34 900-km^2 grid cells is 201 (Francis and Currie 2003: Fig. 1). So, in the Kenyan test, predicted angiosperm family richness per 34 900-km^2 circle can be seen as reasonable if it is greater than actual woody plant family richness but <211 and preferably no more than 201. Similarly, for Africa in general, predicted family richness values using the F&C model should be <202. It is difficult to give a lower bound, but comparison with IGM forecasts could be informative.

The climate data used by Francis and Currie are from global climate databases (i.e., interpreted/interpolated data). The formulation of PET that they used is that of Ahn and Tateishi (1994). Annual water deficit (WD$_{an}$) was calculated as PET$_{an}$ minus mean annual actual evapotranspiration (AET$_{an}$). When using the F&C model to forecast richness in Kenya we used the climate data (and formulations) used by Francis and Currie. This was necessary because the two PET$_{an}$ measures are very different, with ranges of 668–1938 mm and 1177–1727 mm, respectively (Appendix A: Fig. A1). Only in terms of the higher PET$_{an}$ values, which occur in low-elevation interior (xeric) basins and coastal plains, are the two measures similar. For climate stations at higher elevations, and in the mountains and uplands of eastern Africa (>1000 m above sea level), Thornthwaite's PET$_{an}$ is markedly lower than the PET$_{an}$ values of Ahn and Tateishi. Each Kenyan climate station was assigned WD$_{an}$ and PET$_{an}$ values from the location closest to its geographic location (the Ahn and Tateishi data were kriged over a 0.5° grid; these climate data were kindly provided by A. P. Francis and D. J. Currie).

Many of the Kenyan circles overlap (Fig. 2). This would be a problem in model development, but is irrelevant in generating forecasted richness. It is also not important when we consider each circle individually: we simply compare the predicted richness with the actual richness. Similar to confidence intervals, forecasts within one error term (root mean square error) of the original model can be classed as a close fit; those out by 1–2 error terms, a reasonable fit; and those out by >2 error terms, a poor fit. Overlapping circles are a problem, however, if we try to compare predicted with actual values by considering more than one circle at a time (e.g., by correlation). To avoid such pseudoreplication when performing correlation, we generated 30 different random samples of the circles, such that no two circles in any sample overlapped; this produced sample sizes ranging from seven to nine. We correlated actual and forecasted richness values within each sample and report the mean results.

RESULTS

New IGMs

Model coefficients for IGM1 species richness (O'Brien 1998) and all new IGMs are reported in Table 1a, which also gives the R^2 and root mean square error (RMSE) values for the empirical southern African PET$_{min}$ models. In addition, Table 1a gives correlation coefficients for the mathematical transformation of the southern African models into global models (IGMs). In all cases, statistical synonymy ($r > 0.9$) is indicated, making it reasonable to assume that empirical R^2 and RMSE for ideal PET$_{min}$ models also apply to the respective IGMs. In all cases the expected mathematical changes occurred, supporting this assumption (see *Materials and Methods: Development of second-generation Interim General Models*; compare with SAF model coefficients in O'Brien et al. 2000). Furthermore, comparison between IGM1 and IGM2 model coefficients indicates that, consistent with comparisons between

empirical SAF1 and SAF2 models (O'Brien et al. 2000), the addition of topographic range independently increases precision and strength of the model. In all cases, this is shown by an increase in predictive power, reduction in unexplained variance, and the more negative intercept, while the R_{an} and PET_{min} coefficients remain nearly the same.

Statistical results

Spatial pattern of model predictions.—As expected (given the strong correlations between species, genus, and family richness in southern Africa), the patterns of predicted genus (especially) and family richness across Africa were very similar to those for species richness (Figs. 3, 4a, and Appendix A: Fig. A2). Visual comparison of these maps with topographic maps of Africa indicate, consistent with the changes in coefficients (see *Results: New IGMs* and Table 1), that IGM2 predictions result in an increase in forecasted richness values in areas with high topographic relief and a decrease for areas with relatively flat terrain, especially for family richness. For example, Mt. Cameroon, the African Rift Valley, the Ethiopian Highlands, and the Tibesti Dome all exhibit increases in predicted richness, while there are notable decreases in portions of the interior plateaus of eastern and southern Africa, and portions of the Congo and Chad Basins. In between these areas, predicted values remain similar to those generated by IGM1. This emphasizes the independent and idiosyncratic nature of vertical changes in climate and reflects the increased strength and precision of the models. Again in line with the greater contribution that topographic relief makes to the strength and precision of IGM2 for family richness, the most pronounced changes occurred for family richness.

The pattern generated by the F&C model (using the climate station data) is similar to that generated by the IGMs for family richness in that the ordering of predictions is similar (compare Fig. 4a with Fig. 4b). When the 980 climate stations are ranked from lowest to highest predicted value for each model, the mean difference in ranks between the two models is only 65 (although this difference is significant; Wilcoxon signed rank test $Z = 3.6$, $P < 0.001$). The main distinction between the two sets of predictions is in the spread of values. The F&C model predicts high numbers of families under extremely arid conditions (see also Fig. 5). Indeed, all F&C model predictions for Africa are >50 angiosperm families and only 11 points are <70. The maximum predicted value is 186.4, which is only just below the maximum possible from the model (186.8; Fig. 5); 55 predicted values are >175 (there would have been more had we used Ahn and Tateishi PET data in this exercise). In contrast, IGM1 produces 255 predictions below 35 woody plant families, the lowest being 5.8. The maximum predicted value for Africa is 263.9, but only 12 predictions are >175. Some of these differences between the two models relate to the different response

variables, especially at the lowest predicted values. However, the fact that IGM1 predicts substantially more woody plant families in rich cells than the F&C model predicts angiosperm families is a notable difference. IGM2 produces lower predicted family richness at the top end (only six >175, maximum 226.0), and also in the least rich cells (e.g., 12 predictions of zero), but not overall. Mean predictions for the 980 climate stations across Africa are 134.0 (F&C model), 62.6 (IGM1), and 63.0 (IGM2).

Kenyan test.—Predictions of actual woody plant richness values using the two generations of IGMs are mostly reasonable or close fits [within 2 or 1 error term(s), respectively], with a slight increase in precision being found among IGM2 predictions (Table 2a). Using the random sample protocol (see *Materials and Methods: Actual vs. predicted richness for Kenya*) to eliminate pseudoreplication caused by circle overlap, the mean values for ''residuals'' (forecast minus actual values) were very small. Mean observed species richness was 307.2 ± 3.0 (mean $\pm$ SE); the mean residual of the species forecasts for IGM1 was -4.3 ± 3.7 (SD of residual sizes = 71.5 ± 2.4 [SD $\pm$ SE]), and for IGM2 it was 23.1 ± 3.3 (75.2 ± 2.2). Mean genus richness was 172.5 ± 1.4; IGM1 mean residual was -1.4 ± 1.8 (34.0 ± 1.2), and IGM2 mean residual was 10.6 ± 1.6 (34.7 ± 1.0). Mean family richness was 65.4 ± 0.25, IGM1 mean residual was -9.7 ± 0.45 (10.9 ± 0.19), and IGM2 mean residual was -2.7 ± 0.34 (6.2 ± 0.22).

The mean Pearson correlation coefficients between actual and forecast values were high: IGM1 species $r = 0.71 \pm 0.008$; IGM2 species $r = 0.78 \pm 0.007$; IGM1 genera $r = 0.72 \pm 0.007$; IGM2 genera $r = 0.80 \pm 0.006$; IGM1 families $r = 0.68 \pm 0.006$, IGM2 families $r = 0.81 \pm 0.005$. Significance values based on these mean r values and a sample size of eight are marginal for IGM1 ($P \approx 0.05$) and significant for IGM2 ($P \approx 0.02$). Further, the best-fit lines between observed and forecast values for IGM2 approximated the ideal 1:1 line in the cases of species and genera, suggesting no systematic errors in relation to richness levels: mean slope did not differ significantly from 1 nor mean intercept from 0. For families, and for all IGM1 forecasts, the slope (observed values arbitrarily on the *y*-axis) was flatter than 1. (For IGM2, species: mean slope = 0.95 ± 0.03, mean intercept = -6.3 ± 7.3; genera: mean slope = 0.99 ± 0.03, mean intercept = -7.8 ± 4.3; families: mean slope = 0.82 ± 0.02, mean intercept = 14.0 ± 0.9.) Thus the correspondence between observed and forecast richness values was good. Interestingly, ln(topographic range) correlated very strongly with richness values in the random samples: $r = 0.80 \pm 0.005$, 0.83 ± 0.005, 0.86 ± 0.003, respectively, for species, genera, and families ($P \approx 0.01$).

Geographically there was a broad pattern of overprediction in west and northeast Kenya and underprediction in south and central Kenya (Fig. 2). Possible

TABLE 1. Predictive global model specifications for (A) Interim General Models (IGM1 and IGM2), and (B) F&C 2° potential evapotranspiration (PET) model, with values taken from Francis and Currie (2003) and residual mean square errors (RMSE) provided by D. J. Currie.

Model	IGM coefficients ($N = 980$)					Transformation (Pearson correlation r)†
	Intercept (constant)	R_{an} (mm)	PET_{min} (mm)	$(PET_{min})^2$ (mm^2)	ln(topographic range) (m)	
A) Interim general models of the climatic potential for richness: predicting number of woody plant taxa						
IGM1						
Species‡	−150	0.3494	5.6294	−0.0284		0.973
Genera	−70	0.1836	2.9008	−0.0141		0.974
Families	−1	0.0473	0.7197	−0.0039		0.963
IGM2						
Species	−371	0.2987	5.1186	−0.0257	42.7155	0.971
Genera	−170	0.1597	2.6250	−0.0127	19.6916	0.971
Families	−57	0.0372	0.6455	−0.0034	10.1120	0.966
B) Francis and Currie (2° latitude/longitude spatial resolution) global PET model: predicting the number of angiosperm families ($N = 4224$)						
Families	8.8	−0.0641§	0.2199‖	$−6.79 \times 10^{-5}$¶		

Notes: The correlation coefficients indicate statistical singularity ($r > 0.9$) between predictions generated using southern African (SAF) models and those generated using the IGMs, making it reasonable to assume that each IGM is a globally applicable redescription of the ideal empirical relationship obtained for southern Africa (see O'Brien 1998). For the southern African models, numbers in parentheses are the values when negative predictions are converted to zero values (see *Materials and Methods: Development of second-generation Interim General Models*); the first numbers result when the negative values are retained. R_{an} is annual rainfall; PET_{min} and PET_{an} are minimum monthly and annual potential evapotranspiration, respectively; WD_{an} is annual water deficit (see O'Brien 1998).

† Reported for the IGMs are both the empirical relationships obtained for the southern subcontinent of Africa (R^2, adjusted R^2, and RMSE; O'Brien et al. [1998]), and those obtained from mathematical transformation into global models (IGMs for the full range of variation globally in PET_{min}).

‡ See O'Brien (1998).

§ Value reported is WD_{an} (mm), not R_{an}.

‖ Value reported is PET_{an}.

¶ Value reported is $(PET_{an})^2$.

contributing factors are likely to be edaphic ones, with underprediction being associated with richer-than-normal soils (basalt derived) and higher-than-normal soil moisture (presence of lakes, underground water resources, and/or exotic rivers [i.e., rivers bringing water from rainfall elsewhere]), and overprediction being associated with relatively poor soils and low soil moisture (high leaching, lack of exotic rivers or underground water resources). In some cases, overprediction could also be a function of undercollection of botanical specimens (e.g., from remote parts of Kenya), which were the basis for Beentje's maps.

The F&C model appears not to grossly underpredict angiosperm family richness in Kenya (Table 2b). Forecasted values are greater than the number of actual woody plant families in every 34 900-km^2 circle, and greater than the IGM-predicted woody plant family richness (for 25 000-km^2 circles). Given the maximum possible prediction of 187 associated with the F&C model, all forecasted values are less than the total number of angiosperm families known to occur in Kenya (211) and also less than the global maximum number (201) of angiosperm families per 34 900 km^2 reported by Francis and Currie.

Model terms and global application

In terms of global application, the range of variation in annual rainfall and PET_{min} across Africa is representative of the global range of variation in these parameters. Even where $PET_{min} = 0$ (mid latitudes to poles) the IGMs plausibly describe how climate relates to richness, given the use of rainfall rather than precipitation (which includes solid water) as the measure of available liquid water. In other words, if there is rainfall then the energy conditions for liquid water necessarily exist at some time(s) during the year (e.g., summer). Thus R_{an} implicitly (and statistically) measures the amount and/or duration of optimal energy, as well as plant growth, under these conditions (see O'Brien 1998). Thus, where $PET_{min} = 0$, the IGMs still model water–energy dynamics, despite reducing to

$$\text{richness} \propto -a + R_{an}[+\ln(\text{topographic range})]$$

where $-a$ is the (negative) intercept and R_{an} is the mean annual rainfall. Where R_{an} also equals zero, the IGMs reduce to

$$\text{richness} \propto -a[+\ln(\text{topographic range})].$$

In this case zero woody plant richness is expected (e.g., Antarctic), which is empirically plausible.

The IGMs and the F&C model differ primarily in terms of the water variable used and in the sign of the intercept. Francis and Currie use a water-budget variable, water deficit, one of the basic indices of available soil moisture derived from climate (precipitation minus PET). Others are actual evapotranspiration (AET) and

TABLE 1. Extended.

Southern African model fits ($N = 65$)		
R^2†	adj. R^2†	RMSE†
0.788 (0.804)	0.778 (0.794)	73.7 (70.8)
0.798 (0.808)	0.788 (0.798)	36.7 (35.8)
0.697 (0.697)	0.683 (0.683)	11.8 (11.8)
0.856 (0.868)	0.846 (0.859)	61.2 (58.6)
0.868 (0.874)	0.859 (0.865)	29.9 (29.3)
0.815 (0.815)	0.803 (0.803)	9.3 (9.3)
0.837	0.837	17.40

water surplus. All are conditional indices of available soil moisture for plant growth; none is a dynamic climate variable. AET = precipitation only when precipitation < PET. Otherwise, when precipitation ≥ PET, AET = PET. WD = PET − AET when precipitation < PET. When precipitation ≥ PET, WD = 0, because AET = PET. Water surplus = precipitation − PET when precipitation > PET (i.e., when AET = PET and WD = 0). For a detailed analysis of how these indices statistically relate to richness, to climate variables, and

to each other in southern Africa or Africa in general, see O'Brien (1993, 1998).

Since WD = 0 when PET = 0 or when precipitation ≥ PET, the F&C model is a priori conditional. And when $WD_{an} = 0$, the model reduces to an optimal energy model of the relationship of climate with richness, with no water component. For Condition 1, the soil water-budget model, when P_{an} (mean annual precipitation) < PET_{an}, then $AET_{an} = P_{an}$ and $WD_{an} > 0$:

$$\text{richness} \propto a - (PET_{an} - P_{an}) + [PET_{an} - (PET_{an})^2]$$

$$= a - (PET_{an} - AET_{an}) + [PET_{an} - (PET_{an})^2]$$

$$= a - WD_{an} + [PET_{an} - (PET_{an})^2].$$

For Condition 2, the optimal energy-only model, when $P_{an} \geq PET_{an}$ or when $PET_{an} = 0$, then $AET_{an} = PET_{an}$ and $WD_{an} = 0$:

$$\text{richness} \propto a - (PET_{an} - PET_{an}) + [PET_{an} - (PET_{an})^2]$$

$$= a - (PET_{an} - AET_{an}) + [PET_{an} - (PET_{an})^2]$$

$$= a + [PET_{an} - (PET_{an})^2].$$

Thus the F&C model is a soil moisture–energy model where soil moisture deficits limit plant growth and is purely an energy model where water deficits do not occur. Where there is no available water, it predicts between nine and 98 angiosperm families (within the globally observed range of PET_{an}; Fig. 5). This aspect of the model, which derives from both the positive
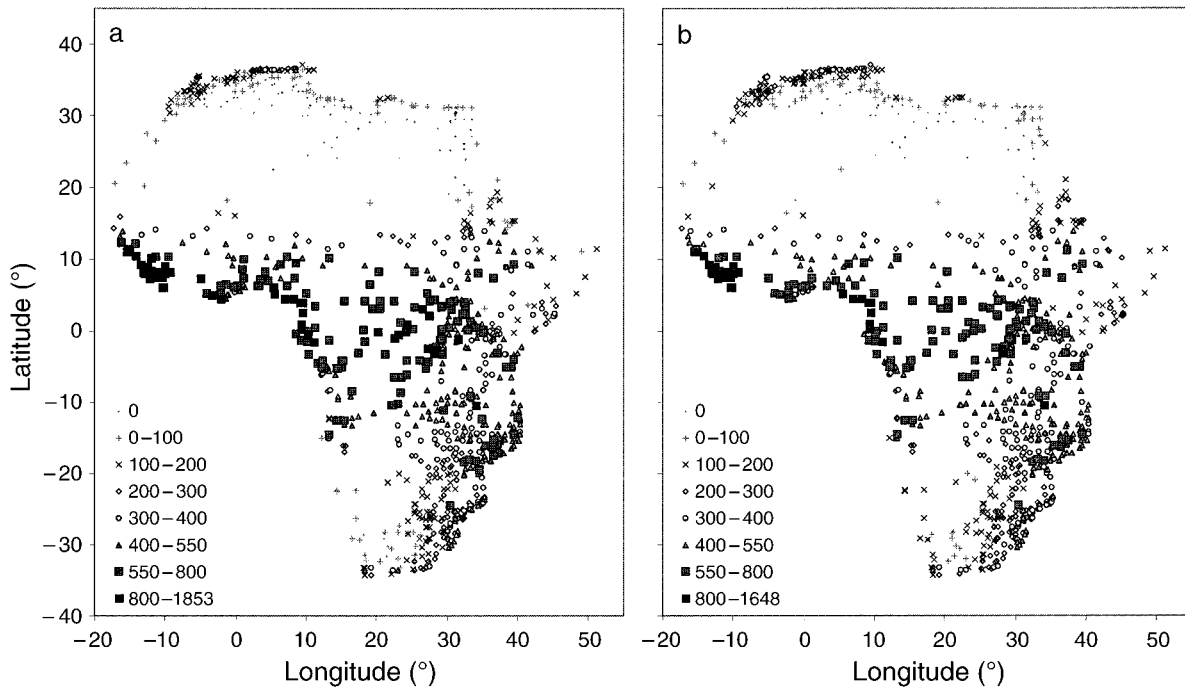
FIG. 3. Predicted species richness for Africa based on (a) IGM1 and (b) IGM2. Values were calculated using the Thornthwaite climate data for all 980 African climate stations (source of climate data: Thornthwaite and Mather 1962–1965). This figure is reproduced in color in Appendix A.
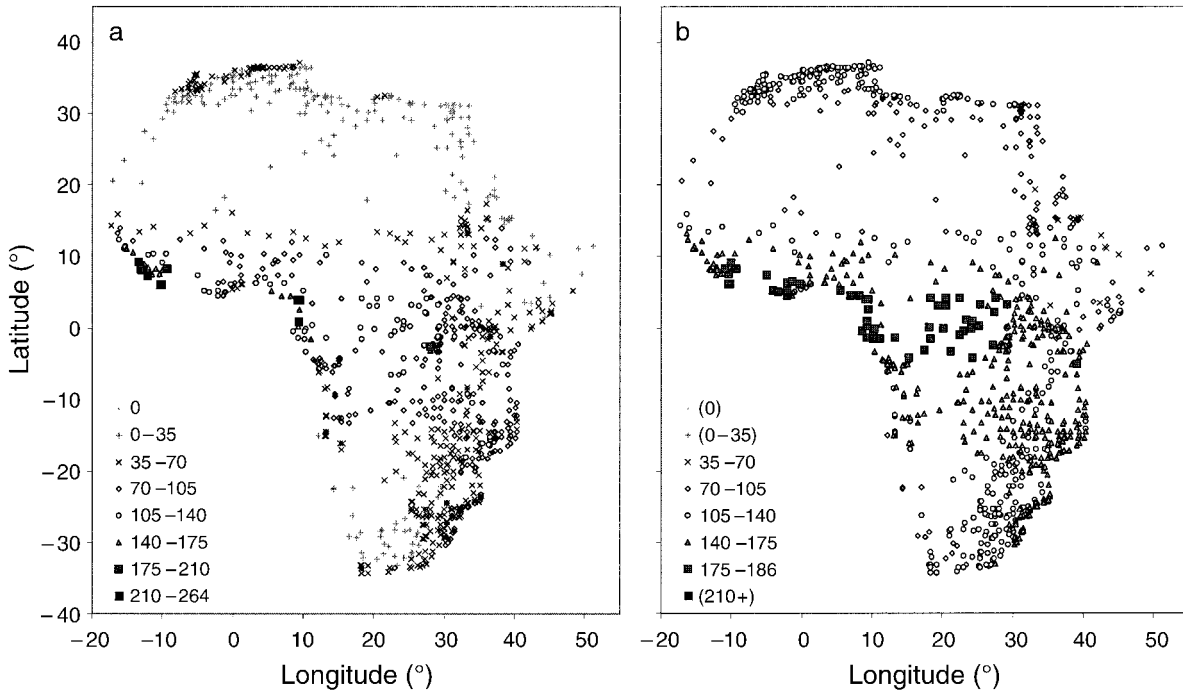
FIG. 4. Predicted family richness for Africa based on (a) IGM1 and (b) F&C model. Parentheses indicate that the category is empty, i.e., no climate stations in Africa have predicted richness within the specified range. Values were calculated using the Thornthwaite climate data for all 980 African climate stations (Thornthwaite and Mather 1962–1965). This figure is reproduced in color in Appendix A. Also, see Fig. A2 in Appendix A for IGM1 and IGM2 predictions at the genus and family levels.

intercept and the values of the other coefficients, suggests that unmodeled effects are subsumed within the statistical fit to the data, and is true for all the Francis and Currie global PET models (from 2° to 10° spatial resolution; Francis and Currie 2003: Table 2). Similarly, interpretation is hindered by the redundancy that results from the collinearity between PET_{an} and WD_{an}.

DISCUSSION

An empirical global model of the climatic potential for richness depends on the quality of the data on which it is based. Systematic and exhaustive species range maps do not exist for humid tropical regions of the world. They do exist for parts of mid to high latitudes (e.g., parts of Western Europe, United States). And they exist for the transition between them (southern Africa, Australia). However, model development also requires regions where we know or can reasonably assume species richness to be on a par with its environmental potential; where recolonization after deglaciation and major volcanic eruption, for example, is most likely to be complete. This assumption seems reasonable with regard to the flora of Africa, given the absence of major physical barriers to migration of species during Plio-Pleistocene ice-age oscillations. It is unreasonable in many parts of the mid to high latitudes. Thus the empirical basis for the IGMs can be considered reasonable.

Empirical performance of the models

The results support the global applicability of the new IGMs of the climatic potential for richness at three taxonomic levels. They support the idea that the relationship between climate and richness stems from the dependence of both climatological and biological dynamics on water–energy dynamics, and that consequent geographic variation in the climatic capacity for biological water–energy dynamics could cause the covariation between realized climate and realized richness. Given that the IGMs apply to the full range of global variation in R_{an} and PET_{min}, reasonable forecasting of the climatic potential for richness is possible for elsewhere in the world. The good fit between actual and predicted richness in Kenya supports this, as does the realistic pattern of relative variation in predicted richness across Africa (see O'Brien 1998). Empirically, the addition of vertical changes in climate in IGM2s alter forecasted richness values almost exclusively in areas of high or low topographic relief, in a positive or negative fashion, respectively. The same should apply globally. Since the IGMs only describe the climate potential for richness, gross over- or underprediction of richness by the models should highlight other variables that need inclusion in a more complete explanation (see *Discussion: Some applications and implications of predictive models*).
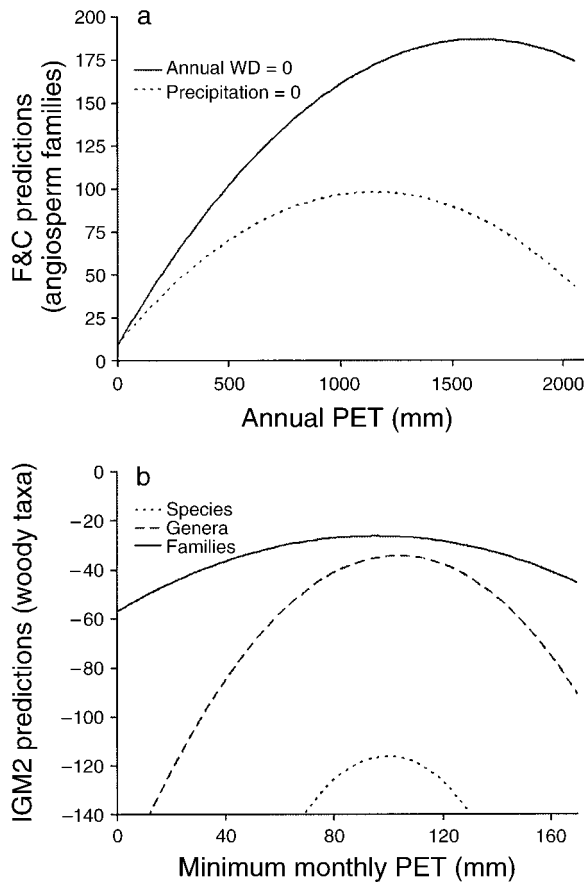
FIG. 5. (a) Envelope of possible predictions from the F&C model (Francis and Currie 2003). The solid line shows the condition of no water deficit (WD) and represents the upper limit of predictions for this model. The dashed line shows the condition of no precipitation and thus represents the lower limit of predictions for this model. All model predictions fall within the area bounded by the two lines. A plot showing the range of predictions of IGM1 can be found in Whittaker et al. (2003: Fig. 7.2b). (b) Predicted values from IGM2 plotted against minimum monthly potential evapotranspiration (PET_{min}) when there is no rainfall and no topography (i.e., completely flat terrain), at the species, genus, and family levels. Note that all are negative, which means that no woody plants are predicted to exist under such conditions, even when optimal energy conditions exist (see *Introduction: Conceptual basis: biological relativity to water–energy dynamics*)—in contrast to the F&C model.

Annual water deficits are common in Kenya and our findings support the predictive usefulness of the F&C model where annual water deficits occur, even in low latitudes.

Comparison of IGMs and the F&C model

To be a general, globally applicable description of the first-order (and ideally causal) relationship of climate with richness, a model should generate reasonable predicted richness values (without regional refitting), and the resulting distribution of relative predicted richness should be similar in pattern and relative magnitude

to observed or expected differences in richness, especially the latitudinal gradient in richness. All work to date suggests that the IGMs meet these and other empirical and theoretical criteria. Our results, together with those of Francis and Currie, suggest that the F&C model also tends to produce a good fit to empirical data in a range of climatic conditions. However, its upper prediction limit of 187 angiosperm families and its positive, often high lower limit (depending on PET_{an}; Fig. 5) suggest that its predictive usefulness is best in moderate (e.g., temperate), rather than harsh (e.g., very arid) or benign (e.g., equatorial humid), climatic conditions.

The F&C model is a purely statistical regression model, which its authors interpret via the importance of secondary or tertiary biotic relationships to climate, such as the correlation of productivity with richness. We have only compared the F&C model with IGM1, since it applies only to the horizontal relationship of climate with richness. Like the other models, the F&C model was limited to a single water variable and a single energy variable (Table 1). In both cases the energy variables are similar (aspects of PET) and related to richness in a functionally similar fashion: an optimal (parabolic curve) function, modeled as $PET - PET^2$. Thus according to both sets of models, richness initially increases and then decreases as energy increases. In terms of climate, such an optimal relationship is empirically plausible with regard to rainfall: as we move from the poles to the tropics, rainfall increases as realized evaporation and the capacity for atmospheric saturation (dew point) increase up to some global optimum. At this point the capacity for evaporation continues to increase but subsequent condensation, saturation, and rainfall decrease as dew point increases. Instead, more and more (and eventually all) evaporated water is held in the atmosphere: the same amount of atmospheric moisture can keep Holland green, but the Sahara a desert.

These similarities between the F&C model and the IGM1 model are considerable and, along with other recent findings (e.g., Hawkins et al. 2003), could suggest that we are close to determining which climatic variables tend to be responsible for constraining plant richness. If so, the differences between the models may be even more instructive and important for advancing our knowledge. In the F&C model, a conditional, non-dynamic soil water-budget variable (WD_{an}) represents available liquid water, as opposed to the dynamic climate variable (R_{an}) in the IGMs. The result is a model of how energy, coupled sometimes with an insufficiency of soil moisture, relates to richness. The conditional rather than general nature of the F&C model can be attributed to at least two factors; (1) the lack of a theoretical or empirical explanatory framework in model development, and (2) statistical issues including multicollinearity between the variables chosen to define climate and how it relates to richness.

TABLE 2. (A) Interim General Models (IGMs): actual, predicted, and ''residual'' values for woody plant species, genus, and family richness/25 000 km^2 ($N = 28$ climate stations). (B) F&C model: actual woody plant richness and predicted angiosperm family richness/34 900 km^2 ($N = 28$ climate stations).

A) IGMs

Climate station	Area (%)	Actual values			Model predictions					
		Woody plant richness			IGM1			IGM2		
		Species	Genus	Family	Species	Genus	Family	Species	Genus	Family
1	100	410	236	83	488	265	83	507	273	88
2	100	508	279	87	437	238	76	468	252	84
3	99	414	237	83	462	251	80	483	260	85
4	100	561	291	91	501	272	84	547	292	96
5	100	160	93	47	187	115	38	182	112	37
6	100	526	286	93	321	179	59	397	213	77
7	100	525	274	87	404	221	72	446	240	82
8	100	560	291	92	347	191	63	417	223	80
9	100	435	247	84	379	207	68	429	230	80
10	95	469	269	84	625	337	101	621	334	102
11	96	413	239	81	720	387	114	704	378	112
12	100	525	274	87	400	218	71	445	239	82
14	88	411	252	79	542	295	89	545	295	91
15	82	408	227	81	486	264	82	528	282	93
16	100	480	249	82	456	248	78	477	257	84
18	88	143	101	56	88	66	23	145	92	37
20	98	460	244	89	322	178	60	368	199	71
23	100	313	184	72	289	160	56	345	186	69
24	100	208	124	58	379	208	68	389	212	70
29	100	525	274	87	383	209	69	427	229	79
30	100	404	232	81	284	157	55	343	185	69
31	100	350	201	78	394	216	70	441	237	81
32	100	486	272	88	318	175	60	386	206	76
33	100	391	220	77	304	168	58	360	194	71
34	100	368	202	81	310	171	59	372	199	73
35	100	477	270	87	359	197	65	422	226	80
36	90	529	277	86	314	175	58	344	188	65
37	100	70	40	24	181	110	38	185	111	39

Notes: Area = percentage of the area of a circle that is land within Kenya. ''Residuals'' = predicted minus actual richness.

In the first case, given an explanatory framework, models can be accepted, rejected, or modified based on theoretical grounds (generality, parsimony, simplicity) and empirical observation, as well as on statistical criteria. Without an explanatory framework, only statistical descriptions of how input data relate to each other are generated, and discrimination of the ''best'' model is restricted to statistical criteria. Empirically the positive intercept of the F&C model suggests that the positive effect of some missing explanatory influence on richness is subsumed in the intercept (when there is no water and no energy, nine angiosperm families are modeled as being present). Within an explanatory framework, this would suggest model rejection, even if alternatives are less powerful statistically.

In the second case, we consider that the F&C model is biased by the fact that water deficit conditions dominate terrestrial systems, as does the vegetation associated with them, with associated richness values constituting the bulk of any global database on richness. A priori redundancy between WD_{an} and PET_{an} increases the statistical precision of this particular relationship at the expense of other possible relationships. Together these biases could account for the high statistical

strength of the F&C model, despite its poor performance under other climatic conditions. Climatic and water-budget variables are meaningful and these meanings need to be considered when modeling how climate relates to biological phenomena; rainfall always measures available liquid water as a function of climate.

Despite these issues, the Francis and Currie (2003) study contributes in several important ways to a better understanding of the relationship of climate with richness. First, their model emphasizes the negative effects of energy in its relationship with richness. It does so in a fashion that is empirically consistent with the optimal relationship between energy and the potential for rainfall (as energy increases, dew point increases while the potential for atmospheric saturation decreases). The same applies with regard to biological dynamics, as shown by the empirical increase and decrease in photosynthesis during the course of a day, and seasonally during the course of a year.

Second, their study highlights an assumption common to many studies of the relationship of climate with richness; that water-budget variables are climate variables. This assumption is similar to treating primary productivity as though it were a dynamic parameter of

TABLE 2. Extended.

	A) IGMs						B) F&C model		
								Actual values	Model predictions
	"Residuals"							Woody plant richness	Angiosperm richness
	IGM1			IGM2					
Species	Genus	Family	Species	Genus	Family	Area (%)	Family	Family
78	29	0	97	37	5	100	85	175
−71	−41	−11	−40	−27	−3	98	88	179
48	14	−3	69	23	2	97	87	172
−60	−19	−7	−14	1	5	100	91	156
27	22	−9	22	19	−10	100	56	77
−205	−107	−34	−129	−73	−16	100	94	158
−121	−53	−15	−79	−34	−5	100	87	152
−213	−100	−29	−143	−68	−12	100	94	150
−56	−40	−16	−6	−17	−4	100	85	153
156	68	17	152	65	18	92	87	183
307	148	33	291	139	31	95	86	185
−125	−56	−16	−80	−35	−5	100	87	152
131	43	10	134	43	12	60	NA	NA
78	37	1	120	55	12	85	84	186
−24	−1	−4	−3	8	2	100	89	145
−55	−35	−33	2	−9	−19	88	59	87
−138	−66	−29	−92	−45	−18	95	89	130
−24	−24	−16	32	2	−3	100	79	151
171	84	10	181	88	12	100	69	155
−142	−65	−18	−98	−45	−8	100	87	152
−120	−75	−26	−61	−47	−12	100	85	151
44	15	−8	91	36	3	100	82	158
−168	−97	−28	−100	−66	−12	100	90	159
−87	−52	−19	−31	−26	−6	95	83	152
−58	−31	−22	4	−3	−8	100	87	150
−118	−73	−22	−55	−44	−7	100	90	157
−215	−102	−28	−185	−89	−21	85	87	141
111	70	14	115	71	15	99	25	95

photosynthesis. The fundamental, dynamic parameters of climate are atmospheric moisture, energy, wind, and pressure. Since derived water-budget variables are subordinate and conditional corollaries of realized climate–soil interactions, it follows that they should be conditional correlates of associated richness. But because they are not parameters of climatological dynamics, it does not follow that they should describe how climate per se relates to richness.

Third, the Francis and Currie (2003) study documents the fact that, when the global variation in PET_{an} is sampled, which is not possible using only African data, an optimal relationship between richness and energy pertains. Thus, Francis and Currie provide the first independent empirical corroboration of the optimal relationship between richness and energy first documented by O'Brien (1989, 1993). It is therefore puzzling that Francis and Currie (2003) argue that their findings refute the existence of such a relationship. Virtually all plant growth depends on liquid water, and since liquid water availability depends on ambient energy conditions, some form of optimal relationship between energy and richness should be expected (to account for the solid and gaseous states of water). It has only recently been documented because few studies sample a sufficient range in climate and richness to obtain the relationship empirically. Most only examine portions of the curve, documenting positive, negative, or insignificant (humid tropics) statistical relationships between energy and richness. These results tend to be treated as competing hypotheses, but our findings and those of Francis and Currie show that they can be reconciled when energy is described as an optimal function.

Fourth, the Francis and Currie study highlights the issue of using only statistical strength to refute a hypothesis. To test the global applicability of IGM1 in principle (see Appendix B), they regressed their family richness data accordingly, as a function of increasing annual rainfall and optimal energy (PET_{min}) conditions. (Note that Francis and Currie cite Legates and Willmott [1992] and Ahn and Tateishi [1994] as the sources of their data; the IGM was derived using climate data from Thornwaite and Mather [1962–1965]). Despite the discrepancies in climate and richness data, they found that this relationship accounted for 63% of the global variation in angiosperm family richness (Francis and Currie 2003:530). This is close to the 68% accounted for

by SAF1/IGM1 for woody plant family richness (O'Brien et al. 1998). Although they rejected IGM1 in favor of the statistically stronger F&C model in this case, their study can be seen as providing the first independent evidence that the IGMs are globally applicable and empirically plausible in principle.

Some applications and implications of predictive models

The most obvious use of predictive models is to predict richness where actual values are unknown. Other applications are also possible. First, if Africa's flora is assumed to be near equilibrium with its climatic potential, the IGMs provide a line of evidence for evaluating whether or not this is the case elsewhere in the world. Second, given that they invoke dynamic climatological parameters, the IGMs can be linked directly to Global Climate Models (GCMs) and used to examine how past and/or future changes in climate could alter present-day richness patterns. Alternatively, being independent of GCMs, they could be used for testing GCM predictions. Perhaps most importantly they can contribute to the development of trans-scalar models, and to making hierarchy theory operational. In essence, when working at more discrete scales of analysis, predictions at the macro scale can be incorporated as constants (''potential richness'') in analyses of how other variables and factors (e.g., edaphics, shade) relate to richness (O'Brien 1989, O'Brien et al. 2000, Whittaker et al. 2001, 2003). In so doing, the first-order effects of climate can be eliminated as active factors, focusing analyses on the residual variation not explained by climate.

In terms of future test implications, gross differences between predicted and actual richness values in Kenya emphasize that climate is not the only factor influencing richness. Consistent with findings for southern Africa (O'Brien et al. 2000), visual examination of topographic, hydrological, and soil maps for Kenya points to edaphic and associated hydrological factors as the next independent parameters that need to be included in a more complete explanation of global variations in plant richness, especially exotic rivers, permanent and ephemeral lakes (pans), ground water reserves, soil parent material, and nutrient content. Of these, exotic rivers, ground water reserves, and soil parent material probably make the most important edaphic contribution to woody plant richness in Africa today, as in the past (O'Brien and Peters 1999a, b). IGMs should grossly overpredict richness where extant richness is below its climatic potential (e.g., where soils are poorer than normal or lower in moisture than that expected as a function of rainfall, and especially where perennial lakes and rivers are scarce). Gross underprediction is expected where perennial lakes and rivers (especially exotic rivers) exist, soils are richer than normal, or soil moisture is greater than that expected as a function of rainfall alone (e.g., due to meltwater).

Conclusions

The results of this study both support and extend the global applicability of O'Brien's (1998) interim general model of the climatic potential for woody plant richness, thereby providing operational versions at three taxonomic levels, for use with or without topographic data. They also support the idea that biological relativity to water–energy dynamics explains the covariation between climate and richness globally, one outcome of which should be a ''latitudinal gradient'' in richness. IGM2 invokes parameters that reflect both the horizontal and vertical vectors of change in climate and should contribute to a better understanding of observed elevational gradients in richness in mountainous regions, as well as idiosyncratic ''hot spots'' of high diversity. Lastly, by providing a systematic and globally applicable model of how first-order differences in climate relate to woody plant richness, we are now in a position to eliminate it as an active factor (hold it constant) when analyzing other causes for differences in richness at more discrete scales of analysis.

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APPENDIX A

Figures showing the relationship between PET data used for IGMs and PET data used for the F&C model for Kenyan climate stations (Fig. A1), the predicted genus richness for Africa based on (a) IGM1 and (b) IGM2 (Fig. A2), color reproductions of Figs. 3 and 4, and associated literature citations are available in ESA's Electronic Data Archive: *Ecological Archives* E086-120-A1.

APPENDIX B

A description of the general methodological constraints, a summary of transformation of southern African models into IGMs, and associated literature citations are available in ESA's Electronic Data Archive: *Ecological Archives* E086-120-A2.

SPECIAL FEATURE

Richard Field, Eileen M. O'Brien, and Robert J. Whittaker. 2005. Global models for predicting woody plant richness from climate: development and evaluation. *Ecology* **86:2263–2277.**

Appendix A. Figures showing the relationship between PET data used for IGMs and PET data used for the F&C model for Kenyan climate stations (Fig. A1), the predicted genus richness for Africa based on (a) IGM1 and (b) IGM2 (Fig. A2), the predicted family richness for Africa based on IGM2 (Fig. A3), color reproductions of Figs. 3 and 4, and associated literature citations.
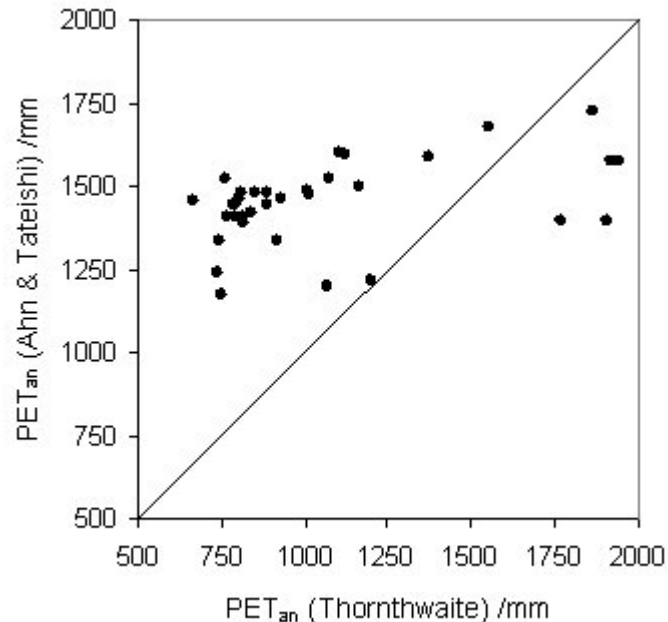
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FIG. A1. Plot of the relationship for Kenya climate stations between PET data used to develop the IGMs (source and formulation: Thornthwaite and Mather 1962–1965) and PET data used for the F&C model (source and formulation: Ahn and Tateishi 1994). NB Whereas PET_{an} (mean annual potential evapotranspiration) values are shown here for the purposes of direct comparison, the IGMs use PET_{min} (minimum monthly mean PET).
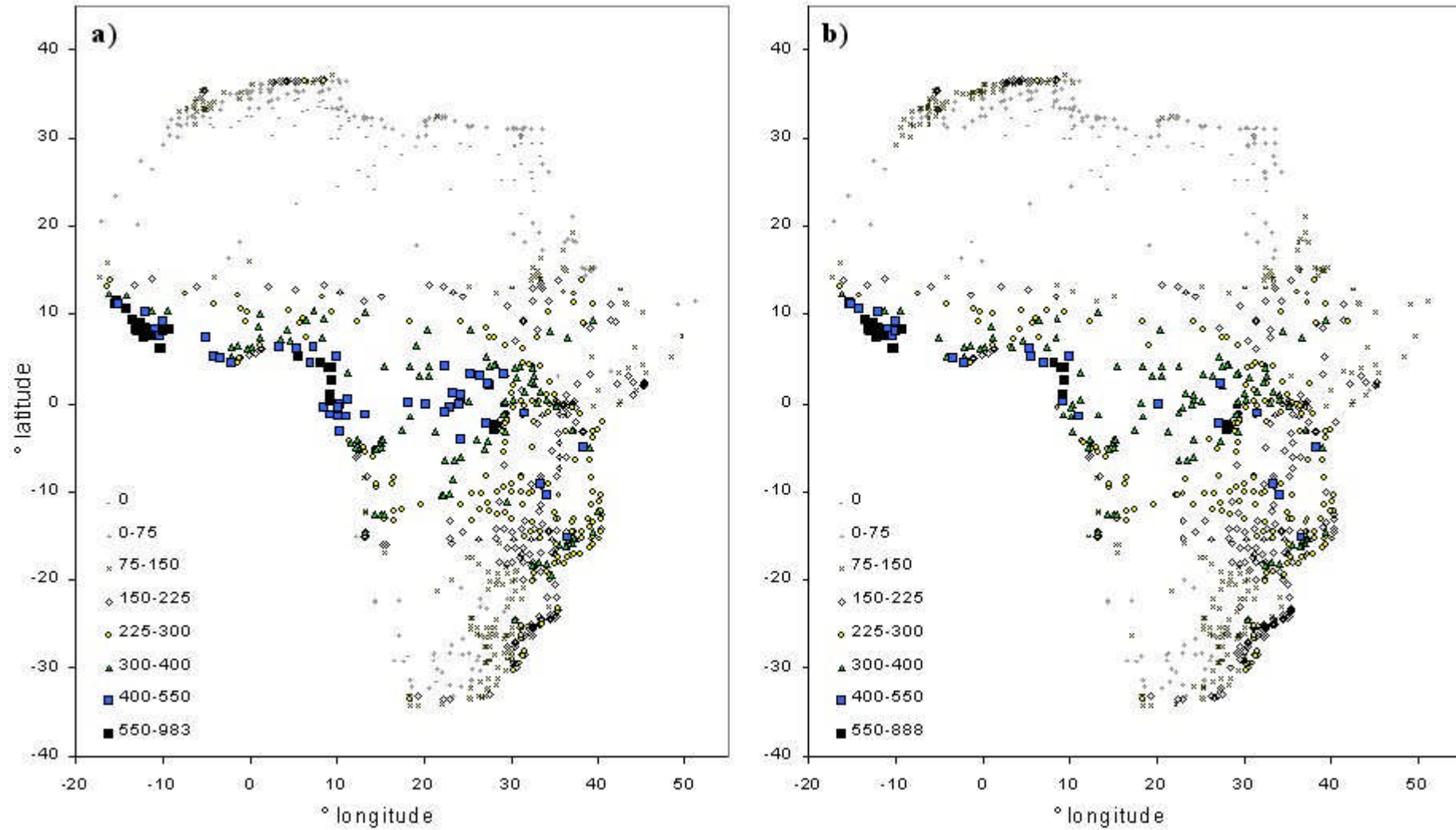
FIG. A2. Predicted genus richness for Africa based on (a) IGM1 and (b) IGM2. Values were calculated using climate data from Thornthwaite and Mather (1962–1965) for all 980 African climate stations.
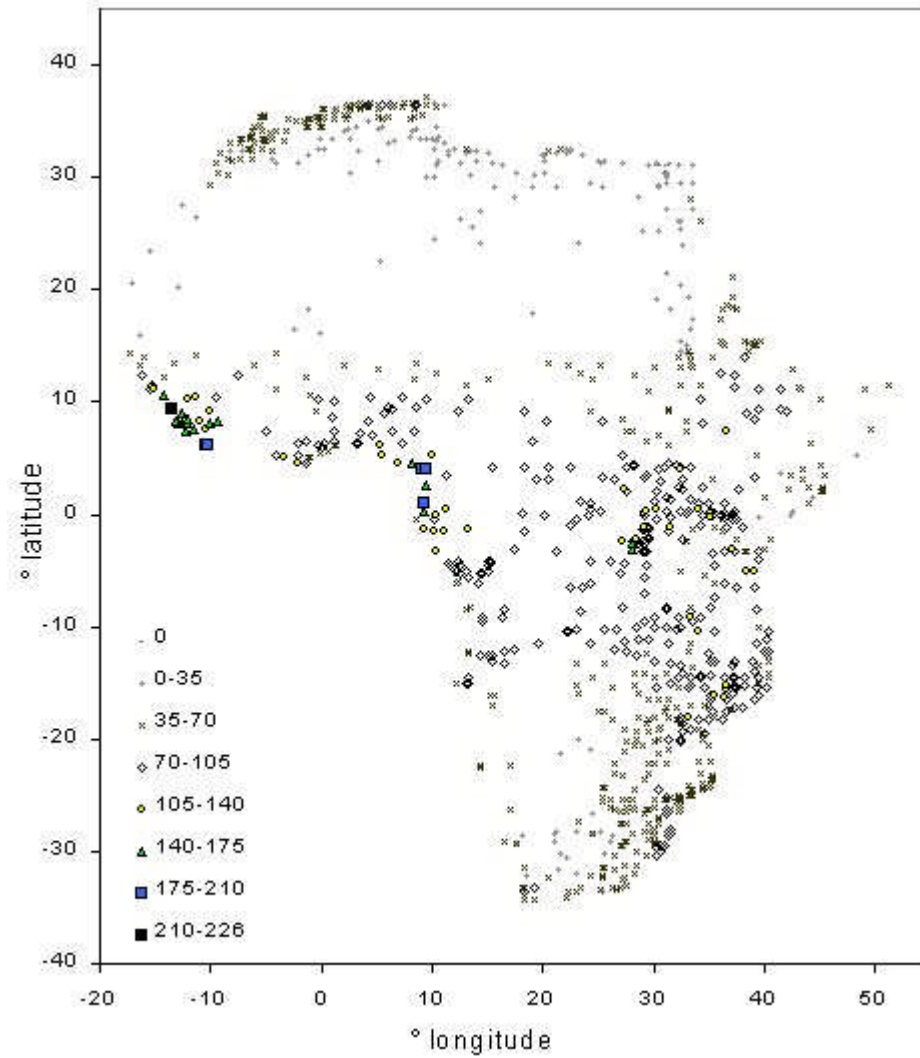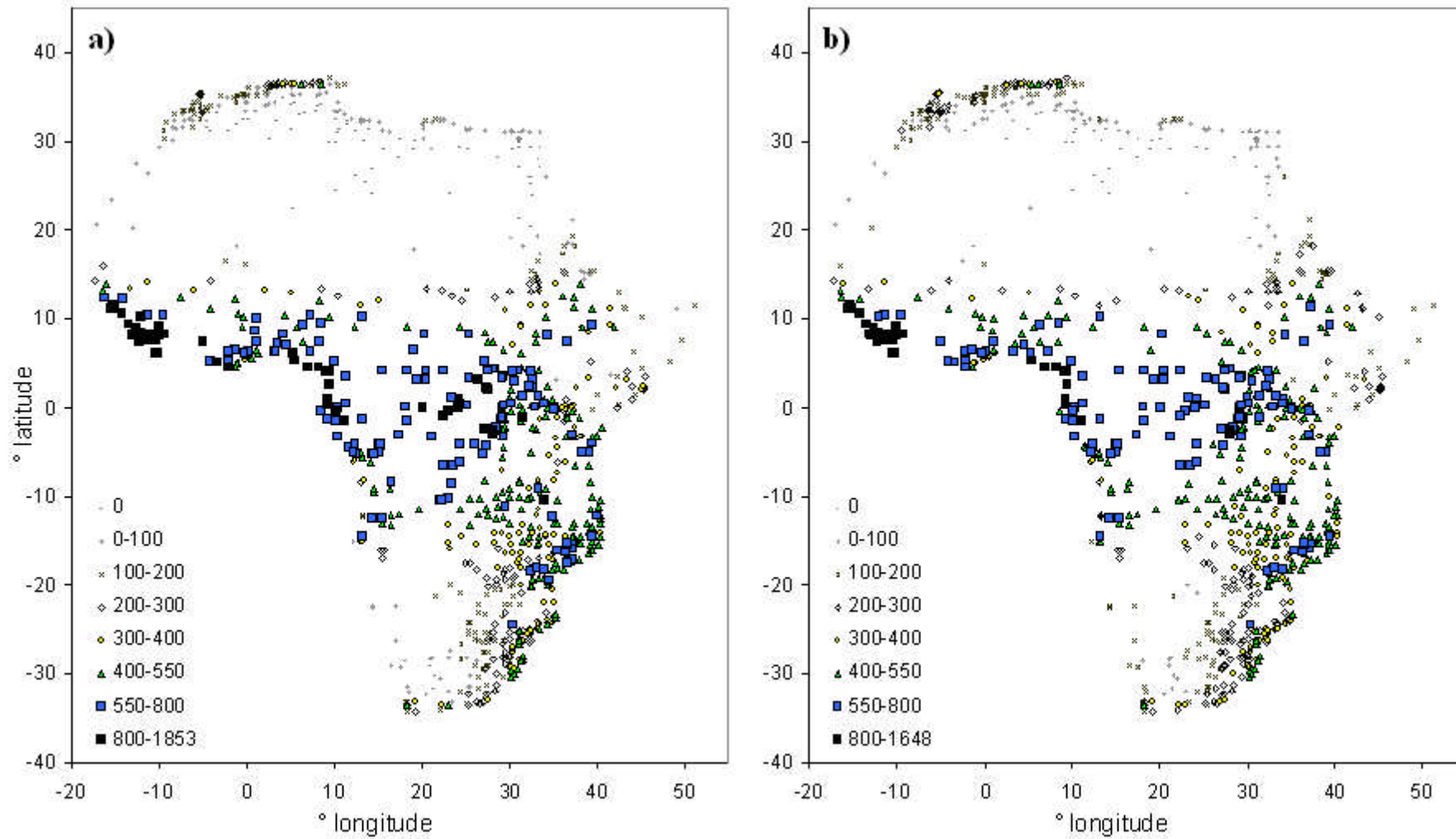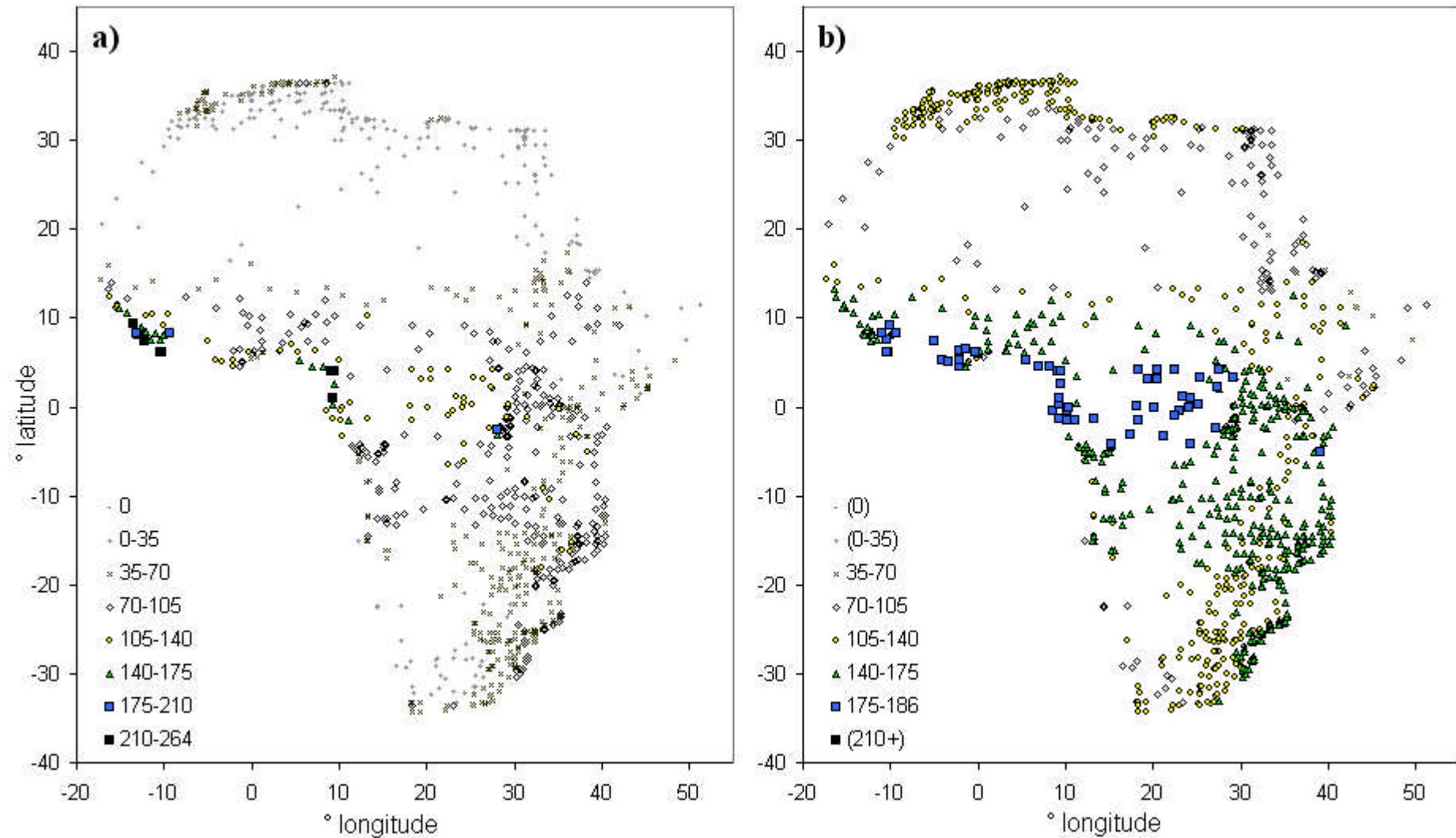
FIG. A3. Predicted family richness for Africa based on IGM2. Values were calculated using climate data from Thornthwaite and Mather (1962–1965) for all 980 African climate stations.

A color version of Fig. 3 from the main article. Predicted species richness for Africa based on (a) IGM1 and (b) IGM2. Values were calculated using the Thornthwaite climate data for all 980 African climate stations (source of climate data: Thornthwaite and Mather 1962–1965).

A color version of Fig. 4 from the main article. Predicted family richness for Africa based on (a) IGM1 and (b) F&C model. In (b), parentheses in the legend indicate that the category is empty; the lowest value predicted by the F&C model is 50.4 angiosperm families (near Mitsiwa, Eritrea) and the highest is 186.4 (Boende, Democratic Republic of the Congo). Values were calculated using the Thornthwaite climate data for all 980 African climate stations (Thornthwaite and Mather 1962–1965). Fig. A2 for IGM1 and IGM2 predictions at the genus level, and Fig. A3 for IGM2 prediction at the family level.

Richard Field, Eileen M. O'Brien, and Robert J. Whittaker. 2005. Global models for predicting woody plant richness from climate: development and evaluation. *Ecology* **86:2263–2277.**

Appendix B. A description of the general methodological constraints, a summary of transformation of southern African models into IGMs, and associated literature citations.

General methodological constraints

Investigating climate's relationship to taxonomic richness is fraught with logistical problems. This begins with the fact that within continental land masses measurable horizontal heterogeneity in climate occurs over distances of at least 100 km (Griffiths 1976), making a sensible minimum sampling area for richness 10,000 km². The data needed to determine richness at this scale are comprehensive sets of species distribution maps. These are rarely available, in practice, being restricted to particular regions or countries (namely, Australia, W. Europe, USA, Canada, southern Africa, and Kenya) and exhaustive only for particular groups of taxa (e.g., birds, mammals, trees). In all cases, richness data derived from range maps are "continuous" over space and necessarily spatially autocorrelated (i.e., the closer samples are, the more similar they are, and vice versa).

In terms of climate, globally representative climate station data have been available since the mid 1960s. In addition to providing "real" (ground-truthed) data, they provide spatially discrete (rather than continuous) data whose spatial distribution are a priori idiosyncratic and independent of environmental parameters, being instead a function of political ones (location of towns, airports, seaports, etc.). Global climate databases also exist. Being based on interpreted (from satellite imagery) and/or interpolated climate station data, they introduce uncertainty with regard to accuracy at ground level. Being continuous rather than discrete data, they are also spatially autocorrelated. Our preference is thus to use climate station data, thereby increasing the reliability of independent variable values while reducing the potential for statistical biases fostered by spatial autocorrelation in associated richness (see below).

A fundamental assumption in climate-richness modeling is that extant richness is on par with its environmental potential. This needs to be kept in mind when selecting a study area and evaluating actual vs. predicted richness, beginning with taxonomic issues.

Unless plant taxonomy is up-to-date, richness values are likely to be inflated since taxonomic "synonyms" have not been identified and eliminated. In this regard, the taxonomy of Africa's flora, for example, is virtually current – revision in line with present-day taxonomic paradigms was completed by the 1990s (e.g., *Flora Zambesiaca*, covering Zimbabwe, Zambia, and Mozambique; *Flora of Southern Africa*, covering Botswana, South Africa, Namibia, Natal, Lesotho, and Swaziland; *Flora of Tropical East Africa*, covering Uganda, Kenya, and Tanzania). Data for Western European, United States (USA), Canadian, and Australian floras are also likely to be current.

Another important taxonomic issue is that the meaning of "richness" is not the same at all taxonomic levels. For plants, richness at the family level reflects the number of successful lineages, not successful forms. Species belonging to a particular genus usually share gross "form" features in common (e.g., all oaks are woody plants, trees/shrubs). Each species, however, expresses discrete biological, ecological or geographical differences in form (e.g., wet- to arid-adapted, evergreen to deciduous trees or shrubs). Thus, although some families

can be monogeneric or even monospecific, in most cases each family represents a spectrum of forms that can range from ephemeral herbs to rain forest canopy trees. In general, if diversity of form is being examined, then species and genus richness are minimum levels of analysis: if diversity of lineage, then family richness is reasonable.

In terms of fundamental factors common to all plants, family richness may actually be ideal since "noise" introduced by biological, ecological, and historical idiosyncrasies associated with the evolution of genera and species is effectively eliminated. Thus, for example, major geological (e.g., orogeny, eustatics, volcanism, plate tectonics, etc.) and global climatological events (e.g., glacial cycles) should be reflected in the global distribution and richness of families, with richness being less than expected as a function of climate alone where such events were followed by or resulted in barriers to dispersal and thus recolonization on par with environmental potential. Focusing on just the last glacial period, for example, even species richness is less than expected in parts of Eurasia where west-east trending mountains impede south-to-north dispersal of taxa. In southeastern USA, the Caribbean Sea and the Gulf of Mexico are dispersal barriers for Neotropical taxa from source areas in Central and South America.

Summary of transformation of southern African models into IGMs

In brief, transformation into IGMs involves three regression models: the "best-fit" southern African model (SAF1/2), which always includes annual rainfall and PET_{min}, and two alternate linear models of climate's relationship to richness in southern Africa (see O'Brien 1998 Appendix for procedures, O'Brien et al. 2000 for all SAF models). Whereas PET_{min}'s parabolic function inhibits extrapolation, the linear function of alternate energy variables permits extrapolation. Based on their relative performance under different climate conditions in southern Africa, a simple "if-then" program implements one of these models to predict richness, and this is done for each of 980 climate stations across Africa. In accord with the mathematical principle of equivalence, these predictions are then re-regressed to re-describe the ideal model for virtually the full range of variation in all independent model parameters, globally: 0 to 4927mm annual rainfall; 6 to 165mm PET_{min}. Given that 0 to 6mm PET_{min} only occurs on the linear, pre-optimum (105mm) portion of the parabolic curve, extrapolation to 0mm PET_{min} is reasonable.

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the origin and robustness of TAR in ecology, even for microorganisms, have been described by García-Martín and Goldenfeld (2006). They postulated that species–area relationships are a general consequence of a species abundance distribution resembling a lognormal distribution with higher rarity, together with the observation that individuals of a given species tend to cluster. These propositions could also be applicable to bacteria in lakes, although more exhaustive studies are needed to corroborate these theoretical questions.

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GLOBAL MODELS FOR PREDICTING WOODY PLANT RICHNESS FROM CLIMATE: COMMENT

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There is abundant evidence that climate strongly influences current patterns of species richness (Wright et al. 1993, Hawkins et al. 2003a), but there have been few attempts to generate global-scale models of climate–richness relationships that can predict richness in areas for which empirical data are lacking or predict how richness will respond to global climate change. One such modeling approach for woody plants was proposed by O'Brien (1993), using gridded species richness and climate data, based on the premise that Thornthwaite's minimum monthly potential evapotranspiration (PET, a measure of winter energy inputs) and liquid rainfall (a measure of water availability) are the key climatic variables that set the environmental capacity for tree richness at the macro scale in southern Africa. O'Brien (1998) subsequently developed the first "interim general

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model" (IGM), derived from the initial southern African model, but with reference to the whole of Africa. O'Brien et al. (1998, 2000) then further modeled southern African woody plants at the genus and family levels (O'Brien et al. 1998) and included topographical relief in all three models (species, genus, and family) to capture orographic effects generating finer scale climatic gradients (O'Brien et al. 2000). Field et al. (2005) recently returned to the protocols developed by the series of papers by O'Brien and colleagues to produce five additional versions of the IGMs, with and without topography, and at three taxonomic levels (species, genus, and family). They also tested the ability of the IGMs to predict woody plant richness patterns in tropical Africa (Kenya) as well as to predict relative richness patterns for the entire continent. Finally, they compared and contrasted the IGMs with a soil water–energy model developed by Francis and Currie (2003) fitted to global angiosperm family richness, the merits of which have also been debated by Qian and Ricklefs (2004) and Currie and Francis (2004).

A key issue with any statistical model designed to explain an ecological gradient is its ability to predict a pattern in regions outside of the original study area. As suggested by their names, the IGMs are intended to predict the pattern and amplitude of tree (and shrub) richness globally. However, although the test of the IGMs using the newer Kenyan data represents an independent test of the models, it remains that they were parameterized and validated using data from within Africa. Further, although IGM1 was previously used to generate maps of the predicted climatic potential for tree species richness in some nontropical regions (USA and China; O'Brien 1998), the predictions could not be validated with data at the same scale as her analysis. Perhaps most importantly, the temperate regions used to evaluate IGM1 do not extend north of 50° N, leaving a significant proportion of the world's landmass beyond the scope of O'Brien's (1998) attempt to examine IGM predictions against existing data. If the IGMs are truly global, ideally they must be shown to provide reasonable predictions in the northern temperate and boreal zones, or at least it must be demonstrated that the underlying logic of the models applies in all climates.

O'Brien (1998) and Field et al. (2005) argued that in mid to high latitudes, where minimum monthly PET equals zero, IGMs can still be used to model tree richness patterns since rainfall, which describes the availability of liquid water, reflects conditions when there is sufficient energy for trees to be active. The idea that (liquid) rainfall can predict plant richness in the far north is in stark contrast to theories claiming that energy drives diversity gradients either via metabolic effects operating at the cellular level (Allen et al. 2002, Brown et

al. 2004) or via a general intolerance of organisms to very cold winter temperatures at high latitudes (Currie 1991, Hawkins et al. 2003b). Given that all previous analyses of plant diversity encompassing high latitudes have included explicit measures of energy either independently of, or combined with, water variables (e.g., actual evapotranspiration [Currie and Paquin 1987], Chickugo's productivity model [Adams and Woodward 1989], a rescaled inverse of annual temperature [Allen et al. 2002], and annual PET or annual temperature [Francis and Currie 2003]), the prediction of Field et al. that tree diversity gradients in cold climates can be reasonably modeled by rainfall alone begs for empirical verification.

We generated a GIS database of tree species in North America and Europe (generally defined as woody plants reaching >4 m in height somewhere within their range). A total of 676 species are represented in North America north of Mexico and 187 species in Europe west of Russia. The latitudinal span of the database is from 25° N to 70° N. Range maps obtained or generated from a variety of sources were digitized in ArcGIS 8.3 (Environmental Systems Research Institute, Redlands, California, USA) and rasterized at 110×110 km grain size. The mapped area includes 1830 cells, 1444 in North America, and 386 in Europe. Details of the sources and maps illustrating the richness gradients will be presented elsewhere.

Following O'Brien (1998) and Field et al. (2005), we calculated the minimum monthly potential evapotranspiration (hereafter PET_{min}) using Thornthwaite's formula (Thornthwaite 1948, Bonan 2002), and rainfall was estimated as total precipitation for all months with a mean temperature above 0°C. We also calculated ln(transformed) elevation (derived from GTOPO30 digital elevation model [DEM] data with a horizontal grid spacing of 30 arc-seconds (*available online*),[3] maximum monthly PET and annual PET (calculated as above), and annual temperature (*available online*)[4] as potential predictors of tree species richness. Finally, we estimated the potential growing season as the number of months when mean temperature was >0°C.

Because the IGMs are parameterized for tree and shrub richness, whereas our database comprises only trees, we cannot directly compare observed vs. predicted richness values using our richness data. More importantly, our climatic data are gridded and interpolated, whereas Field et al. (2005) based their analysis on weather station data, and a precise test of the parameterized IGMs would require that our climatic predictors be measured with the methods used by Field

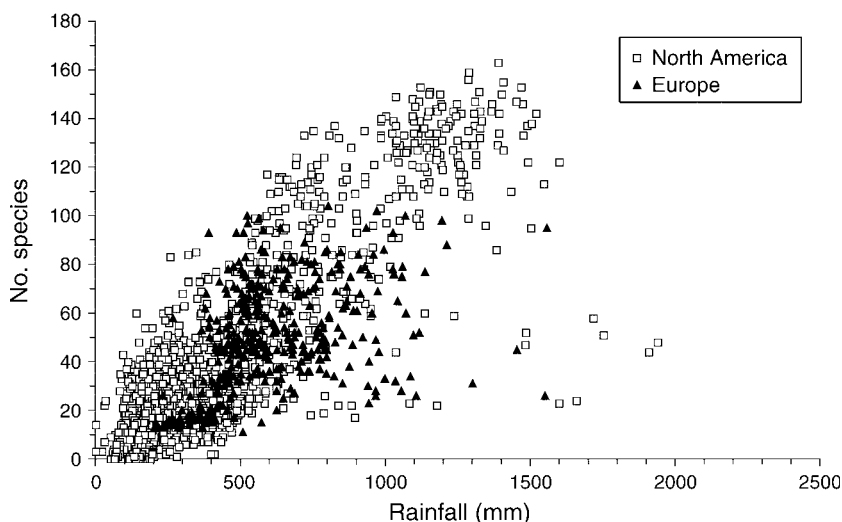[3] ⟨http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.html⟩
[4] ⟨http://www.grid.unep.ch/data/summary.php?dataid=GNV15⟩

Fig. 1. Relationship between annual rainfall (precipitation falling in months with an average temperature >0°C) and tree species richness in 110 × 110 km cells in North America and Europe. Coastal cells with land areas <50% of inland cells have been excluded.

et al. However, although we cannot generate predicted values for each IGM against which to compare observed richness, we can test the prediction that rainfall accounts for tree richness better than energy in temperate climates. As far as we know, the "water–energy dynamics" hypothesis underlying the IGMs is the only theory for diversity gradients that makes this prediction; thus, this represents a relatively strong test of the hypothesis. We test this using reparameterized equivalents of the IGMs that contain combinations of the variables predicted to explain diversity.

We first tested the independent contribution of the energy component of the IGMs (PET_{min}) to tree richness across both regions, which we expected to have limited explanatory power given that it has a value of zero in 77.1% of our cells (80.6% of the North American cells and 63.5% of the European cells). It explained 18.5% of the variance. We then tested a model equivalent to a "reduced" IGM1 containing rainfall alone and found that it accounted for 64.1% of the variance in tree richness. Further, the relationship is linear throughout the full range of the data (Fig. 1), indicating that rainfall statistically explains tree richness in Alaska as well as in Alabama, USA. There are noticeable outliers in both North America and Europe (Fig. 1), which in the former case are all Pacific Northwest coastal cells located between Oregon and southern Alaska (where trees may be unable to respond to the massive amounts of rain falling within a short growing season), but in Europe the outliers are scattered throughout the continent. Despite these outliers, the prediction that rainfall limits tree richness even in extremely cold climates is broadly supported. This is further confirmed by adding PET_{min}

and ln(range in elevation) to the model (thus generating the equivalent to a reparameterized IGM2). This model explained 65.1% of the variance, only 1.0% more than the reduced IGM1.

The ability of liquid rainfall to explain statistically almost two-thirds of the variance in tree richness across two continents dominated by cool climates seems to confirm the logic underlying the IGMs as argued by O'Brien (1993, 1998) and Field et al. (2005). But even if true, we note that the coefficients of determination of the IGMs vary between regions: the fitted IGM2 explains 78.8% of the variance in southern Africa and 79.1% of the variance in Kenya, whereas in the Holarctic the fitted equivalent of IGM2 explains 65.1% of the variance (almost all due to rainfall). The reduced fit in the Holarctic could be due to the use of an inappropriate measure of energy (PET_{min}) when climates are cold, or to the influences of factors found in the north that do not operate in Africa (a possibility also noted by O'Brien [1998]), especially in Europe. Although not discussed by Field et al. (2005), O'Brien (1998) recommended that when PET_{min} is <14 or >45 mm and rainfall <1000 mm, the maximum monthly PET (i.e., energy input in the summer) should be used rather than the minimum monthly PET. In the Holarctic 95.2% of the cells have PET_{min} of <14 or >45, and 90.5% have rainfall <1000 mm, so we used PET_{max} to generate a modified equivalent to IGM1, which increased the explanatory power of the model to 64.7%, only 0.6% more than the rainfall model. We also converted annual temperature using one of the linear transformations dictated by metabolic theory ($1000/[T + 273]$; Allen et al. 2002) and added it to the rainfall model to investigate its ability to

improve the predictions. However, it explained only an additional 1.2% of the variance, so temperature provides no explanatory power beyond that provided by rainfall (it independently explained only 21.8% of the variance in richness). Finally, we examined annual PET (which by itself explained 44.7% of the variance in tree richness) and found that it improved the coefficient of determination of the rainfall model to 0.681, enough to suggest that energy input summed over the entire year has a measurable effect on tree richness independently of summer conditions. Even so, it appears that using a range of measures of energy does not greatly improve the fit of the models, so additional processes unrelated to contemporary climatic conditions may be operating in the temperate zone (e.g., Pleistocene glaciation cycles, edaphic effects, or human impacts). Future research can explore this issue.

Given the clear importance of rainfall to tree richness gradients over this span of latitudes, it is also necessary to ask if richness is most strongly associated with the total amount of rainfall falling over the growing season or, as alluded to above with respect to the Pacific coast, if the length of the growing season itself is what matters. Growing season varies substantially between Alaska and Florida (or Norway and Greece), and annual rainfall is greater towards the south partially as a consequence of the extra time over which water accumulates. Indeed, there was a strong correlation between length of growing season and annual rainfall ($r = 0.800$), indicating that the latter contains an implicit energy component. However, growing season length explained substantially less of the variance in tree richness than rainfall (47.7% vs. 64.1%, respectively), and adding growing season to the rainfall model increased the coefficient of determination by only 0.007. So, tree richness appears to be associated more with the total amount of rain than with the length of time over which the rain falls. It is important to note that this does not mean that energy does not influence tree richness, only that it is not critical to include an explicit energy variable in climatically based models.

In sum, the logic underlying the IGMs is able to explain the broad species richness patterns of trees reasonably well in regions strikingly different climatically from the regions used to generate the models, and the supposition of O'Brien (1998) and Field et al. (2005) that summer rainfall by itself represents a reasonable predictor of tree diversity in northern latitudes is confirmed. Thus, we have an independent validation of the explanation for woody plant species richness gradients developed by O'Brien (1993, 1998) and Field et al. (2005). Of course, contemporary climate cannot explain everything, since climate models, including the IGMs, lack the speciation–extinction dynamics that are needed to link the past with the present. Even so, if we want to understand how currently existing tree species distribute themselves geographically, "water–energy dynamics" seems to offer a useful conceptual and empirical framework.

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GLOBAL MODELS FOR PREDICTING WOODY PLANT RICHNESS FROM CLIMATE: REPLY

Richard Field,[1,3] Eileen M. O'Brien,[2] and Chris P. Lavers[1]

Hawkins et al. (2007) have provided strong and significant empirical support for water–energy dynamics, and thus climate, being a fundamental factor limiting the global distribution of terrestrial plant richness, as outlined in Field et al. (2005). Contrary to common expectations, Hawkins et al. find that rainfall, not energy, appears to be the most significant factor in the mid-to-high latitudes. In so doing they lend further empirical support to the global applicability of the Interim General Models (IGMs; O'Brien 1998, Field et al. 2005) and to the theoretical premise underlying this relationship: biological relativity to water–energy dynamics (O'Brien 2006). For a trans-scalar model of how spatial variation in water–energy dynamics might translate into richness patterns, see Lavers and Field (2006).

IGM-1 and IGM-2 of the climatic potential for richness are of the form

$$\text{species richness} \propto -a + R_{an} + \text{PET}_{min} - (\text{PET}_{min})^2$$

$$[+\ln(\text{range in elevation}), \text{IGM 2 only}]$$

where a is a constant, R_{an} is mean annual rainfall, and PET_{min} is minimum monthly potential evapotranspiration.

One inherent prediction of the IGMs is that rainfall alone (as opposed to precipitation) should predict reasonable, if not close fit, richness values if PET_{min} is zero. This includes mid-to-high latitudes, where the energy conditions associated with liquid water (optimal energy) do not occur year round: water is often frozen,

unlike in lower latitudes. In such areas, the horizontal energy component in the IGMs is redundant. The vertical energy parameter (topographic relief) remains as a dynamic parameter, though the effect of variable elevation when water is frozen at sea level is qualitatively different from its effect when energy is optimal. In mid-to-high latitudes, rainfall tends to increase with ambient energy during the course of a year; if PET never exceeds zero then all water on land is ice. In other words, rainfall incorporates the most biologically important part of abiotic energy in colder climates (Field et al. 2005), and so should produce a good fit with tree richness in mid-to-high latitudes. Hawkins et al. (2007) test this idea with tree richness and climate data for 12 100 km^2 equal-area grid cells covering North America and Europe ($N = 1830$). Although they did not analyze how well IGMs predict richness (due to differences in the response variable), they did analyze the significance to tree richness of the different parameters included in IGMs as well as other traditional models, such as annual PET, annual actual evapotranspiration (AET), and annual temperature. Annual AET, as expected for this part of the world, is the strongest single correlate of richness across the whole study area ($r = 0.84$ compared with $r = 0.80$ for rainfall). However, as outlined in Field et al. (2005), it is not a climate variable but an outcome of climate (atmospheric water–energy dynamics governing precipitation and potential evapotranspiration) that is used to index the soil water budget. Hawkins et al. (2007) found that, contrary to common belief, rainfall is a much stronger correlate of richness than pure energy variables (temperature, PET).

Rainfall (liquid water) is a significant factor at all latitudes, increasingly so where energy limits water availability seasonally (both at low latitudes where energy can be excessive and at mid-to-high latitudes where it can be insufficient). The results that Hawkins et al. (2007) report add empirical support for the optimal nature of the relationship of energy not only with the capacity for water to do work, but also with life's capacity to do work (O'Brien 2006). Where (and when) PET_{min} exceeds zero, horizontal variability in energy conditions (positive–negative energy effects) is essential to explaining richness gradients (O'Brien 1993, 1998). It drives all work done by water in two ways: first, via the capacity of water to do work molecularly, including changes in state; and secondly, via the hydrologic cycle, which drives atmospheric thermodynamics and heat exchange globally. This should lead to underprediction by the rainfall-only model where $\text{PET}_{min} > 0$. In these areas of underprediction, we expect energy variables to be important.

The data used by Hawkins et al. (2007) contain some interesting geographic patterns that they do not mention, but which are relevant to what they say. Using the same data (kindly provided by Bradford A.
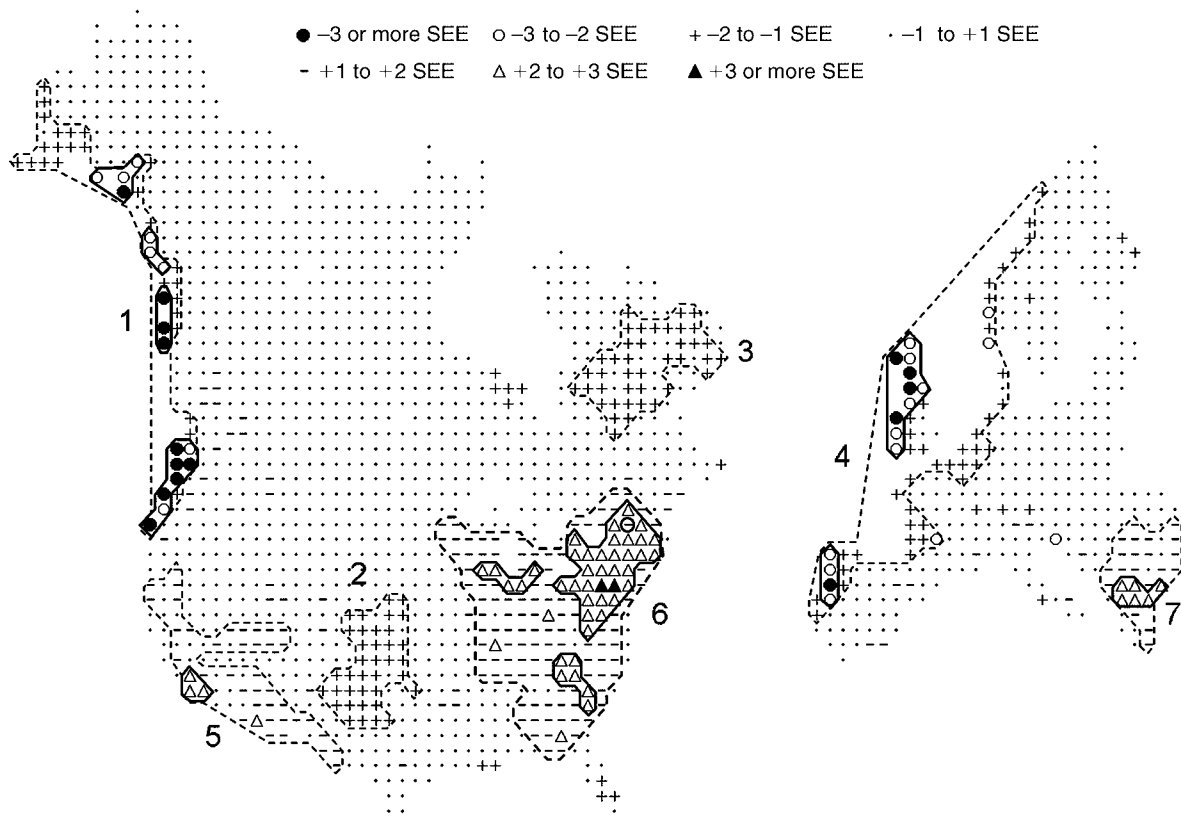
Fig. 1. Map of the residuals from the cross-continent regression of tree species richness on mean annual rainfall, with grain size = 12 100 km^2. Residuals are shown in seven categories, according to the size of the error relative to the standard error of the estimate (SEE) of the model. More than two standard errors represent a gross error of fit. Seven spatial clusters of residuals are identified on the map and are discussed in the text. Circles and plus (+) signs represent overprediction by >1 SEE (negative residuals); triangles and minus (–) signs represent underprediction by >1 SEE (positive residuals), consistent with O'Brien et al. (2000). Clusters are identified as spatially aggregated cells that are reasonable fits (observed richness within 2 SEE of the fitted value; dashed lines) surrounding clusters of cells with gross errors of fit (>2 SEE; solid lines). All clusters of overprediction consist entirely of cells with negative residuals; all cells in the clusters of underprediction have positive residuals except for three cases in cluster 5.

Hawkins), we re-ran their analysis and mapped the residuals, in the same way that O'Brien et al. (2000) did. We briefly discuss the salient features of the resulting map. Hawkins et al. intend to publish a fuller analysis of their data, so we limit our focus to the residuals from the regression of tree richness on rainfall, which Hawkins et al. (2007) performed.

Fig. 1 shows the residuals from the cross-continent rainfall model reported by Hawkins et al. (2007). We identified four clusters of negative residuals and three clusters of positive ones, all of which are remarkably spatially coherent. The negative residuals (clusters 1–4) indicate overprediction: fewer tree species are present than are expected from the cross-continental fit between tree richness and rainfall. The positive residuals (clusters 5–7) show underprediction: more species are present than are expected from rainfall alone. Clusters were identified on the basis of residuals that differ from fitted values by more than one standard error of the estimate

(SEE, or RMSE root mean square error). Only residuals greater than 2 × SEE are considered gross errors of fit. Those within 1–2 SEE are considered "reasonable fits" and those within 1 SEE "close fits."

The two largest regions of overprediction (clusters 1 and 4) are the west coasts of the two continents, north of about 40° N. Both contain cells that are reasonable fits (observed richness within 2 SEE of the fitted value) surrounding cells with gross errors of fit (>2 SEE). The other clusters of overprediction (clusters 2 and 3) are the southern Great Plains of the United States and the far eastern part of Canada. Neither contains gross errors of fit; instead, these clusters comprise reasonable (<2 SEE) but not close (<1 SEE) fits, markedly clustered spatially rather than randomly distributed. The largest region of underprediction (cluster 6) is the deciduous forest biome of the eastern United States, including the Appalachians. The chaparral regions of the southwestern United States and the Balkan peninsula of Europe are

TABLE 1. Summary statistics for the cells with overprediction and underprediction of tree species richness from the rainfall model.

Error category	N	Richness	Predicted	Rainfall	PET	PET$_{min}$	AET	TOPOG
A) Means (overall, Europe + North America)								
−3 SEE +	15	36.5 (3.3)	134.0 (6.7)	1485 (75)	490 (59)	8.9 (1.7)	374 (33)	1240 (253)
−3 to −2 SEE	21	35.5 (3.9)	89.3 (3.5)	985 (39)	421 (48)	6.5 (1.6)	341 (34)	979 (278)
−2 to −1 SEE	160	27.1 (1.6)	54.0 (1.7)	590 (19)	558 (26)	3.7 (0.6)	441 (16)	593 (59)
−1 to +1 SEE	1373	35.4 (0.8)	37.1 (0.7)	402 (8)	530 (8)	1.8 (0.1)	396 (6)	682 (20)
+1 to +2 SEE	206	93.2 (2.5)	62.1 (2.3)	681 (26)	884 (15)	3.8 (0.4)	629 (17)	849 (60)
+2 to +3 SEE	53	117.1 (2.8)	66.0 (2.9)	725 (33)	819 (23)	2.6 (0.8)	679 (24)	780 (91)
+3 SEE+	2	134.0 (1.0)	66.9 (1.5)	735 (17)	771 (6)	0.0	737 (5)	645 (39)
Overall	1830	43.7 (0.8)	43.7 (0.7)	475 (8)	579 (7)	2.3 (0.1)	434 (5)	704 (18)
Clusters								
B) Means (within clusters, with |residual| >2 × SEE)								
1	18	34.4 (3.6)	115.5 (8.8)	1278 (98)	488 (50)	5.4 (1.6)	369 (32)	1835 (289)
4	17	34.1 (2.2)	98.0 (4.1)	1082 (46)	407 (58)	10.2 (1.6)	332 (37)	332 (55)
5	4	78.0 (6.0)	24.9 (4.1)	266 (46)	1139 (103)	15.5 (3.2)	346 (23)	2585 (201)
6	45	124.1 (2.4)	72.4 (2.5)	796 (28)	793 (21)	1.5 (0.6)	739 (19)	628 (65)
7	6	95.8 (1.3)	45.9 (2.2)	500 (24)	788 (19)	1.4 (1.4)	470 (24)	669 (65)
C) Means (full clusters)								
1	47	24.1 (2.4)	71.4 (6.4)	785 (72)	404 (31)	2.2 (0.7)	327 (18)	1996 (183)
2	40	22.5 (1.8)	48.1 (1.6)	524 (18)	985 (20)	2.4 (0.4)	637 (18)	413 (27)
3	49	16.1 (0.7)	39.5 (0.7)	428 (8)	345 (9)	0.0	359 (7)	439 (23)
4	60	36.8 (1.3)	75.5 (2.4)	831 (27)	413 (27)	8.6 (0.8)	341 (16)	233 (31)
5	59	54.1 (2.2)	27.3 (1.9)	292 (21)	1130 (16)	7.1 (0.8)	346 (13)	1976 (102)
6	158	120.8 (1.7)	83.1 (1.8)	915 (20)	856 (13)	3.6 (0.4)	784 (12)	415 (29)
7	29	82.7 (2.1)	49.9 (1.6)	545 (18)	710 (12)	1.3 (0.6)	492 (17)	460 (56)

Notes: Values shown are means and SE (in parentheses). Explanation of variables: N, number of cells; rainfall, mean annual rainfall (mm); PET, mean annual potential evapotranspiration (mm); PET$_{min}$, minimum monthly mean PET (mm); AET, mean annual actual evapotranspiration (mm); TOPOG, range in elevation (m). (A) Across the whole study area, cells for which fitted richness values differ from actual richness by the number of standard errors of the estimate (SEE) are indicated in the first column. (B) Within the clusters (shown in Fig. 1; cluster identity number is shown in the first column), only those cells for which there is a gross error of fit (i.e., the absolute residual is more than twice the SEE). (C) The entire clusters, including cells with close fits (<1 SEE), reasonable fits (<2 SEE), and gross errors of fit (>2 SEE).

also underpredicted. Some details of the clusters are given in Table 1. Clusters 1 and 4 both have relatively high rainfall, typically far in excess of PET, which is low; thus much of the water tends to be runoff unused by trees. This is likely to reduce the fit between rainfall and tree species richness. The data set comprises cells with >50% land area, so that there is some potential for species–area effects. Within cluster 1 there is a positive correlation ($r = 0.55$) between the residuals from the cross-continent rainfall model and cell area; there is a corresponding but weaker correlation ($r = 0.36$) within cluster 4. A third, small region of slight overprediction (not identified as a cluster) is in Florida, where it is very wet, but PET is high, so that AET is relatively close to PET. This region is also very flat. In cluster 6 AET is close to PET, and there is year-round precipitation, suggesting that most of the water can be used by plants. Within this region the correlation between rainfall and tree species richness is very strong and linear ($r = 0.87$), but the (extrapolated) intercept is high and positive, suggesting that some other factor(s) is increasing richness at all rainfall levels. Interestingly there is no correlation between topography and richness in this region; the same is true for cluster 5. In contrast, the region of overprediction in the Balkans of Europe

(cluster 7) has quite a weak correlation between richness and rainfall ($r = 0.45$), but quite a strong one ($r = 0.66$) with ln(range in elevation).

Examination of the clusters of overprediction and underprediction suggests a range of factors that might help to explain the deviation from the overall rainfall relationship, including seasonality, human activity, and glaciation history. Some of the clusters are suspected to be "impoverished," having fewer species than expected from their climate (e.g., the United Kingdom, in cluster 4). The southern Great Plains region (cluster 2), although in reasonable accord with its climatic potential, is well known to have lower than expected tree richness, not because of climatic conditions, but because of a long history of burning (e.g., Mann 2005, and references therein; though burning was practiced over a much wider area than that covered by cluster 2). Across the other clusters ($N = 402$ cells), annual actual evapotranspiration (AET) is very strongly correlated with species richness ($r = 0.91$). The equivalent correlation with annual potential evapotranspiration (PET) is weaker, but still strong ($r = 0.64$), and virtually identical to that with annual temperature ($r = 0.63$). The correlation with PET$_{min}$ is very weak ($r = -0.15$), but consistent with the fact that near-freezing minimum temperatures dominate

the study area: most PET_{min} values are zero. The correlation with ln(elevation range) is minimal and not significant. This is not unexpected, since the relationship between elevation and richness is indirect, via its relationship with energy (and thus water–energy dynamics), and is consistent with earlier analyses (e.g., O'Brien 1993, 1998, O'Brien et al. 1998, 2000). These results, together with those of Hawkins et al. (2007), serve to emphasize that, although the critical variable is liquid water, its capacity to do work is always a function of ambient energy conditions (O'Brien 1993, 1998, 2006). Since spatial variability in energy parameters should always be associated with spatial variability in water–energy dynamics, measures of ambient energy help to account for the spatial patterning of tree species richness in regions where the rainfall model produces a poor fit: relatively localized parts of the continents. However, as found by Hawkins et al., pure energy variables (e.g., PET or temperature) alone do not capture the relationship between living organisms and abiotic water–energy dynamics at the cross-continent scale.

The foregoing analysis furthers the potential for operationalizing hierarchy theory: once climate can be accounted for, we can move from the macro scale to meso and micro scales of analysis and analyze variation in richness while holding climate constant. In other words, we advocate starting with climate when trying to understand and model terrestrial species richness. Other parameters and dynamics should come into play progressively, in a hierarchical and trans-scalar fashion (e.g., O'Brien et al. 2000, Whittaker et al. 2001, O'Brien 2006).

The results of Hawkins et al. (2007), and those presented here, bring to the fore another key point with regard to developing general explanations and global models of climate–richness relationships. An underlying assumption in analyses of climate–richness relationships is that the distributional ranges of species (and thus the geography of richness) reflect climatic potential. Otherwise the samples are not representative of the relationship between climate and richness, which is likely where the flora and its richness are still recovering from glaciation. This is one of the main reasons why O'Brien (1993, 1998) used southern Africa to develop empirical relationships and Africa to develop general relationships. In empirical work, areas for which the assumption is clearly unreasonable may be excluded from analyses *that aim to determine the equilibrial relationship of climate with richness*. A byproduct of this practice is that, once the role of climate has been identified, it can then be held constant when examining how other factors relate to richness (O'Brien 1998). Within the region covered by the data set of Hawkins et al. (2007), actual richness is known to be less than potential richness as a function of climate alone on the west coasts of Europe and northern North America (O'Brien 1998). If these areas (clusters 1 and 4) are excluded from the data set, the cross-continent rainfall model accounts for 77% ($N = 1723$) of the variance in tree species richness, considerably more than the 64% ($N = 1830$) reported by Hawkins et al., and more even than AET (72%; $N = 1723$).

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