

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_iiia/datasets/a13/fnoc.html)

⁴ (<http://www.grid.unep.ch/data/summary.php?dataid=GNV15>)

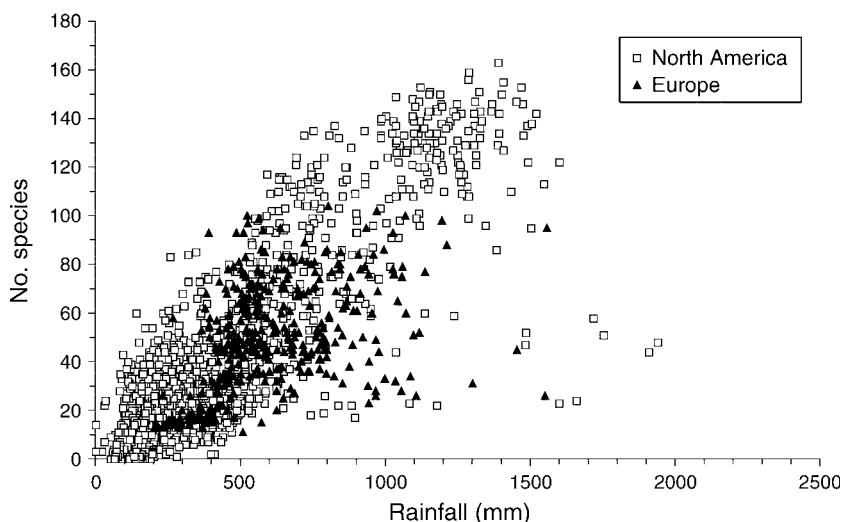


FIG. 1. Relationship between annual rainfall (precipitation falling in months with an average temperature $>0^{\circ}\text{C}$) and tree species richness in 110×110 km cells in North America and Europe. Coastal cells with land areas $<50\%$ of inland cells have been excluded.

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 $\ln(\text{range in elevation})$ 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

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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

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

[+ln(range in elevation), 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 km² 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 $\text{PET}_{\text{min}} > 0$. 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.

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