

DOES ECOSYSTEM SIZE DETERMINE AQUATIC BACTERIAL RICHNESS? COMMENT

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In their paper “Does ecosystem size determine aquatic bacterial richness?” Reche et al. (2005) observed a significant correlation between lake surface area and lake bacterial OTU (operational taxonomic unit) richness in 32 lakes. The authors propose that this relationship corroborates one of the predictions of the island-biogeography theory, i.e., that larger islands support more species than smaller islands (MacArthur and Wilson 1967). The results of Reche et al. (2005) have already been cited in support of a positive relationship between habitat size and bacterial taxonomic richness (Bell et al. 2005, Dolan 2005). We argue that the study by Reche et al. (2005) does not provide support of a causal relationship between bacterial richness and habitat size, since their conclusions are biased by incorrect merging of data sets that are not comparable and because the methods used to determine bacterial richness are not adequate.

The significant correlation between lake area and bacterial OTU numbers obtained by Reche et al. (2005) was based on data from three separate papers (Lindström and Leskinen 2002, Zwart et al. 2002, Reche et al. 2005). Treated separately, the data from Lindström and Leskinen (2002) and Zwart et al. (2002) show no significant correlation between lake area and number of OTUs detected ($P = 0.40$ and $P = 0.20$ respectively; linear correlations of log-transformed data) while the data from Reche et al. (2005) are almost significantly correlated ($P = 0.072$). When these three data sets are merged, the correlation becomes significant ($P < 0.001$), as reported by Reche et al. (2005).

In two of the data sets (Lindström and Leskinen 2002, Reche et al. 2005), OTU richness was determined by

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counting the number of bands formed in denaturing gradient gel electrophoresis (DGGE). This method is commonly used in microbial ecology to obtain an image of microbial community structures (e.g., Forney et al. 2004, Loisel et al. 2006). Some of the limitations of DGGE are briefly discussed by Reche et al. (2005), for instance they acknowledge that DGGE in the best case only reflects the most dominant taxa. However, the consequence of bacterial community structures being skewed with few abundant and many rare taxa, a quite likely scenario (Acinas et al. 2004, Venter et al. 2004, Gans et al. 2005), is not addressed. If a low fraction of the present populations was detected, a change in the number of DGGE bands could reflect a change in rank-abundance of populations (i.e., in the number of populations above the threshold of detection) rather than a change in richness (Forney et al. 2004). Thus, the number of DGGE bands may provide a biased estimate of richness, since it also depends on the evenness of a community. Furthermore, a recent study combining numerical simulations with laboratory experiments (Loisel et al. 2006) demonstrates that the number of bands or peaks obtained using DGGE and similar methods is not related to the richness of communities. Instead, the number of OTUs detected saturates around 35. Thus, the number of DGGE bands is a poor estimator of community richness.

In the third data subset used by Reche et al. (2005), i.e., the data from Zwart et al. (2002), OTU richness is represented by the number of unique bacterial 16S rRNA sequences obtained from seven different studies screening clone libraries from nine lakes. Bacterial OTU numbers as determined by DGGE band numbers appears to saturate around 35 as reported by Loisel et al. (2006). In contrast, the number of unique sequences obtained from clone libraries from similar communities can be much greater. In the data set compiled by Zwart et al. (2002) the number of unique sequences per lake ranged from six to 125, the average being 60. Therefore clone library data are not comparable with DGGE data, and accordingly these two types of data should not be merged. Further, the available data (six lakes) from the original references in Zwart et al. (2002) show that the clone libraries screened range largely in size, at least from 45 to 350 clones per lake. Since the number of OTUs, or unique bacterial 16S rRNA sequences, from each lake was not corrected for sample size (i.e., number of clones picked) we suspect that the reported OTU richness reflects the effort spent by the respective researcher rather than community richness. Therefore, these data are not suitable for analysis of how lake surface area or other parameters are related to bacterial richness.

If the two remaining data sets from Reche et al. (2005), i.e., the DGGE data sets, are merged there is a significant correlation between DGGE band numbers and lake surface area (linear correlation of log-transformed data, $P = 0.002$, $r^2 = 0.379$, $n = 23$). Although DGGE band numbers do not reflect richness of a community, and it is unclear what it reflects as discussed above, a significant correlation between DGGE band numbers and lake surface area might still have some ecological meaning. However, we question the merging of these two datasets into one analysis. One-way ANOVA analyses show that DGGE band numbers differ significantly between the two sub-studies ($P = 0.004$), and there was also very little overlap in lake sizes between sub-studies (0.0001–0.02 and 0.01–6.2 km², respectively; $P < 0.001$). Hence, it is plausible that a significant correlation between lake area and DGGE band numbers was obtained only because both lake area and DGGE band numbers depended on sub-study, and instead alternative explanations to the relationship found should be evaluated.

The laboratory protocols used in the two sub-studies differed (Lindström and Leskinen 2002, Reche et al. 2005). For instance different primer pairs were used, and thereby most likely different bacterial populations were detected (see, e.g., Forney et al. 2004). Thus, due to the differences in methodology, the two different studies could have had different resolution and/or thresholds of detection in their estimates of numbers of DGGE bands. Further, we cannot exclude that the Spanish high mountain lakes studied by Reche et al. (2005) for some other reason than lake area harbored bacterial communities giving rise to fewer bands than the communities in the Swedish and Norwegian lakes studied by Lindström and Leskinen (2002). Thus, we cannot tangle out which factors cause the difference in number of DGGE bands between the two sub-studies. However, it is clear that lake surface area is not the only possible explanation, and there is no solid support for the idea of a causal relationship between lake surface area and DGGE band numbers.

To summarize, we argue that it still remains to be shown if ecosystem size determines aquatic bacterial richness.

Acknowledgments

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DOES ECOSYSTEM SIZE DETERMINE AQUATIC BACTERIA RICHNESS? REPLY

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Lindström et al. (2007) found two major objections to our paper (Reche et al. 2005) on the relationship between bacterial richness of operational taxonomic units (OTU) and lake size. First, from a methodological perspective, they argue against the use of the number of

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bands in the denaturing-gradient gel electrophoresis (DGGE) as a proxy for bacterial OTU richness. Second, from a more theoretical perspective, they criticize the causal nature of the relationship between OTU richness and lake size.

To rigorously determine bacterial richness, as the number of species in a given ecosystem, both a precise definition of species and a total success in the DNA recovery using molecular tools are required. Species definition is controversial even for eukaryotes (Mayden 1997) and is especially controversial for prokaryotes (Rosselló-Mora and Amann 2001). Rosselló-Mora and Amann trust the phylo-phenetic species definition for bacteria based mostly on pragmatic and well-defined reasons. Diversity can be studied using any kind of unit, as long as the definition is clear and used consistently in all the study systems (Hughes et al. 2001). With polymerase chain reaction (PCR)-dependent DGGE techniques, only the taxa comprising more than 1% of the total targeted cells can be detected, and those less than 0.1% are difficult to retrieve. Certainly, DGGE technique is not the perfect determination for the total number of species present but we argue (e.g., Casamayor et al. 2000) that the number of visible bands in denaturant gradient polyacrylamide gels is a viable metric for community structure.

Recently, Pedrós-Alió (2006) suggested the distinction between the concepts of biodiversity (total genetic information) and diversity (the components that are active and abundant at one particular time and place) proposed by Margalef (1994, 1997) and its potential application to microbial diversity studies as a way out for this methodological impasse. Some species are present over time with high abundance and are probably responsible for ecosystem function. Magurran and Henderson (2003) called these “core” species. The remaining species with low abundance and sporadic appearance are “occasional” species. Consequently, the number of bands obtained for a given lake may reflect the number of core species or lake diversity sensu Margalef, so long as the sampling effort is comparable. The number of DNA bands in DGGE could determine the richness of core species or, with less semantic risk, OTU richness with the caution that this number is not the absolute number of species or lake biodiversity.

Another reticence of Lindström et al. on the association between number of bands in DGGE fingerprinting and the OTU richness is based on the results obtained by Loisel et al. (2006). They found that the maximum number of bands saturated about 35 and alleged that some bands can represent more than one phylotype due to co-migration (fuzzy-wide bands). In our study, the samples neither from the high mountain lakes nor from the boreal lakes (Lindström and Leskinen 2002) showed more than 16 bands, far from the upper limit proposed by Loisel et al. (2006). In

relation to the supposing occurrence of bands including co-migrating phylotypes (fuzzy-wide bands), these phylotypes will likely represent “sibling” species (analogous to the different species belonging to a genus) and, then, each band will correspond to a higher taxonomic resolution (i.e., OTU will represent genus equivalents). Horner-Devine et al. (2004) obtained significant taxa–area relationships (TAR) using multiple OTU definitions (95%, 97%, and 99% sequence similarity). This range of definitions can be considered analogous to different taxonomic resolutions (for example, TAR for genus, species, and subspecies, respectively). Their results support the consistence of TAR, although they interestingly obtained different slopes (z values) and significance levels for each taxonomic resolution.

Lindström et al. disapprove the data merging (i.e., our own data and Lindström and Leskinen [2002] and Zwart et al. [2002] data) that generated the significant OTU richness–lake-area relationship based on the different techniques used in each study. Generally, to get ecological patterns using literature data it is necessary to surrender to a miscellany of techniques. Of course, the ideal situation is to use data obtained with identical techniques, nevertheless, once a pattern emerges, the presumption is that the pattern is strong enough despite the noise associated with multiple techniques. Indeed, a significant relationship ($n = 22$, $r = 0.616$, $P = 0.0017$, $z = 0.085 \pm 0.023$ [mean \pm SE]) is also obtained when we used exclusively the more comparable data that use DGGE fingerprinting (Lindström and Leskinen 2002, Reche et al. 2005). Therefore, we have little doubts about the existence of a pattern between the number of DGGE bands and the lake size. In addition, other studies using a unique technique (e.g., Horner-Devine et al. 2004, Bell et al. 2005, van der Gast et al. 2005) have reported relationships between ecosystem size and bacteria richness in different ecosystems, reinforcing the robustness of this pattern. We believe that the debate should address mechanisms that generate this pattern, the z values variability across ecosystems or sampling conditions, the limits where TAR can be found, and so on.

Under this motivation, Woodcock et al. (2006) point out that a proper understanding of microbial TAR seems unlikely without an appropriate appreciation of sampling considerations. Current microbial data are obtained from very small (clone libraries) or truncated (fingerprinting methods) samples. However, it is inconceivable that microbial ecologists will be able to verify patterns by a complete census (biodiversity sensu Margalef) with actual molecular techniques. Since the species evenness and spatial clustering can profoundly influence the shape of TAR (He and Legendre 2002, Green and Ostling 2003), the awareness of the importance of both sample definition and sampling will strengthen the search for microbial patterns under comparable conditions. Recently, some evidences on

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>)

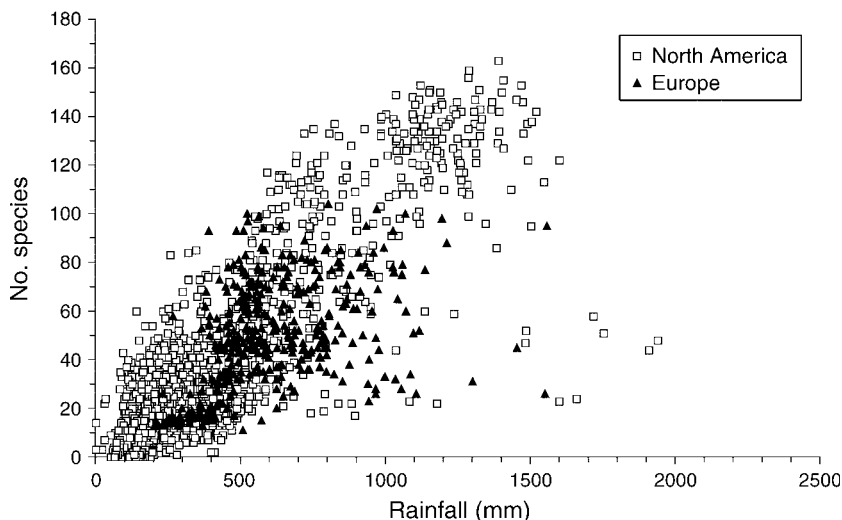


FIG. 1. Relationship between annual rainfall (precipitation falling in months with an average temperature $>0^{\circ}\text{C}$) and tree species richness in 110×110 km cells in North America and Europe. Coastal cells with land areas $<50\%$ of inland cells have been excluded.

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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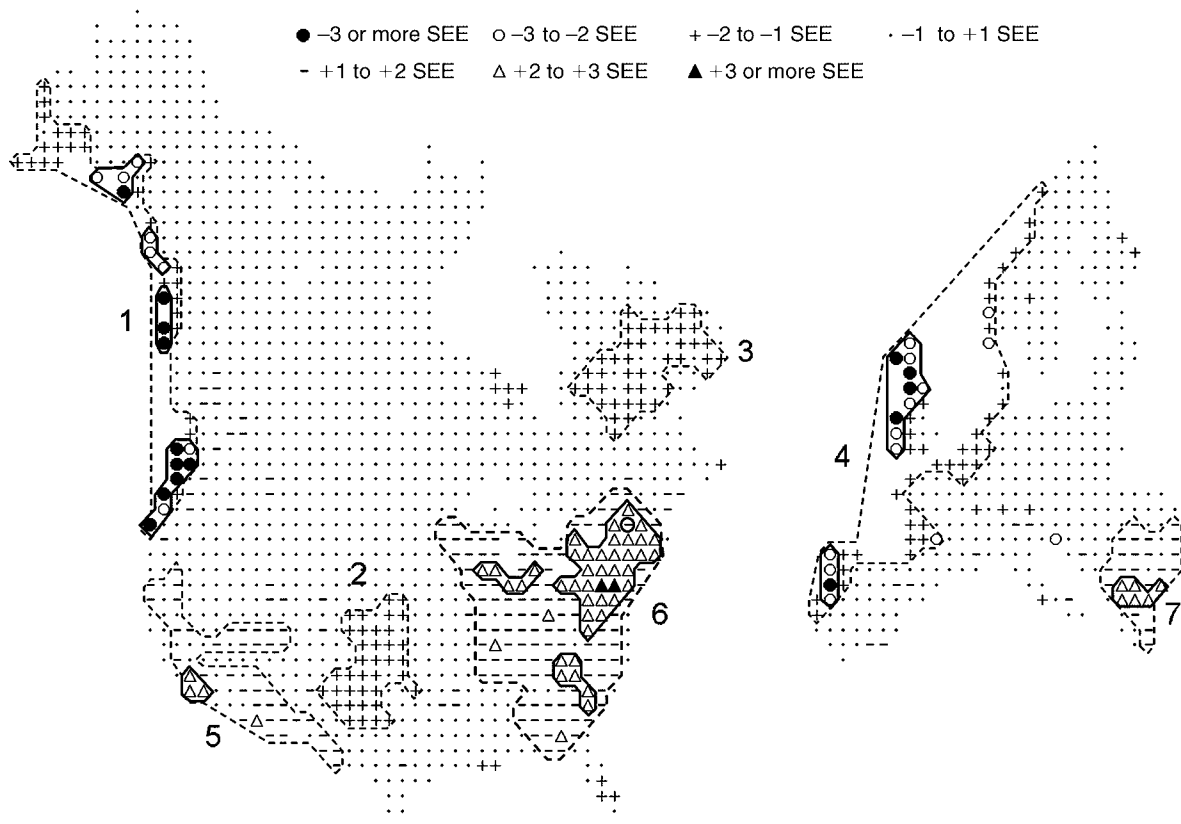


FIG. 1. Map of the residuals from the cross-continent regression of tree species richness on mean annual rainfall, with grain size = 12 100 km². Residuals are shown in seven categories, according to the size of the error relative to the standard error of the estimate (SEE) of the model. More than two 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 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 $2 \times \text{SEE}$ 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	<i>N</i>	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 (16)	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 $\ln(\text{range in elevation})$.

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