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Scale Dependence of Species-Energy Relationships: Evidence from Fishes in Thousands of Lakes

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ABSTRACT: Variation in the shape of relationships between species richness and different measures of energy may be linked to variation in the spatial scale on which such relationships are measured. We examine scale dependence in the relationship between potential evapotranspiration and the species richness of fishes in 7,885 postglacial lakes. The strength of this relationship is weak across lake communities but strong and positive across groups of lakes or regions. In addition, the strength and slope of this relationship increase significantly as the regional scale of analysis is increased. We interpret the observed patterns in terms of a simple model whereby energy influences the linear character of the species-energy relationship through its influence on spatial turnover in the species composition (beta diversity). Our results suggest that if energy is strongly tied to patterns of site occupancy or abundance, the parameters of species-energy relationships will depend, to a considerable extent, on the scale of measurement. Furthermore, the ability of high-energy regions to accommodate relatively large numbers of rare or infrequent species may underlie any general tendency for the strength or shape of species-energy relationships to change with scale.

Keywords: species richness, species-energy relationships, potential evapotranspiration, spatial scale, beta diversity, fishes.

The role of energy in accounting for the heterogeneous distribution of species richness across the earth has been a core focus of ecology (Rosenzweig 1995; Gaston 2000; Evans et al. 2005), and patterns of species richness have been tied more consistently and convincingly to energy

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than to other factors (Wright et al. 1993). Decades of investigation have revealed, however, that there is a great deal of variation in the shape of species-energy relationships (Mittelbach et al. 2001), and their underlying mechanisms have remained largely unresolved (Currie et al. 2004; Evans et al. 2005).

Some variation in the shape of species-energy relationships is undoubtedly due to differences in the scale of measurement, like variation in many other ecological patterns (Levin 1992). Species-energy relationships may differ depending on whether they are assessed at small grain sizes (e.g., a few square kilometers or less) or large ones (hundreds of square kilometers or more) and are more likely to be positive and linear in the latter case (Evans et al. 2005 and references therein; see also Gaston 2000), especially when species have a common historical context and potentially confounding areal and sampling effects are controlled for (see Abrams 1995). Thus, the grain of an analysis—that is, the size of the geographic units for which species richness is estimated—can influence the form of the relationship between species richness and energy (Scheiner et al. 2000) and has received explicit attention in a growing number of investigations (e.g., Lyons and Willig 2002; Scheiner and Jones 2002; van Rensburg et al. 2002; Bailey et al. 2004; Chalcraft et al. 2004; Storch et al. 2005; Harrison et al. 2006). Grain size will delimit the mechanisms that mediate the interaction between species richness and energy (Tonn 1990; Kaspari et al. 2003). In particular, processes that influence species survival within communities are important in determining the nature of the species-energy relationship at a grain size of a single community or smaller, while consequences of these processes for spatial turnover in species composition come into play when regions or groups of communities are compared (Scheiner et al. 2000; Chase and Leibold 2002). An understanding of the link between species turnover and regional variation in species richness is, furthermore, vital for an understanding of large-scale biodiversity patterns (Ricklefs 2004). We investigate the influence of spatial grain on the form of species-energy relationships, and we use the terms "scale" and "grain size" interchangeably.

Another important aspect of spatial scale, the "extent" of an analysis, is generally related to grain but not explicitly considered here.

The manner in which the spatial grain might influence the form of species-energy relationships to become more positive and linear at larger grains can be illustrated using an additive partitioning of components of species richness (Lande 1996):

$$D_\gamma = \overline{D_\alpha} + D_\beta. \tag{1}$$

Here gamma diversity D_γ, the species richness of a region, is the sum of alpha diversity $\overline{D_\alpha}$, average community species richness, and beta diversity D_β, the average number of species not found in a single randomly chosen community (Veech et al. 2002), a measure of turnover in species composition. Suppose that a landscape is divided into a set of "regions" that define the grain of a particular analysis, each containing multiple communities (e.g., regions could be equal-area quadrates). Beta diversity does not contribute to the species richness of regions whose communities are identical in composition. If there is dissimilarity among communities ($D_\beta > 0$), D_β contributes to regional richness and to its variation. Let us assume that regions have approximately the same number of communities and that energy has a positive and linear effect on D_β; it follows that high-energy regions will tend to have more species than low-energy regions (given that there is no strongly negative interaction between the D_β and $\overline{D_\alpha}$). The effect of energy will depend on the number of communities that regions have; that is, if regions have only a small number of communities, D_β will constitute a relatively small component of regional richness, and any positive effect of energy on D_β will be concomitantly small. But as the number of communities within regions increases, the relationship between species richness and energy will become more linear because regional richness increasingly reflects the influence of energy on the D_β component. The linear effect of energy on D_β is due to energy's influence on the rate of sample-based species accumulation, with communities constituting samples. If the first community counted within a region is typical, its species richness will be the $\overline{D_\alpha}$ component of regional richness; communities added thereafter will account for the D_β component, as illustrated in simplified form in figure 1A. The divergence of species accumulation curves—which measures the influence of energy on D_β—will increase as regional richness is counted from increasing numbers of communities. There are two aspects to this linear response: first, a linear model will explain a greater proportion of the variation in richness as more communities are sampled because of the increasing importance of D_β (on which the linear effect acts) relative to $\overline{D_\alpha}$; second, the slope of the linear model will

increase because the divergence of species accumulation curves produces an increasing gradient in species richness across regions of different energy. While this model is framed in terms of numbers of communities, it implies scale-dependent variation in the linear character of species-energy relationships because the number of communities within regions will generally be related to the size of the regions (i.e., grain size). Note that scale dependence arises only if energy influences $\overline{D_\beta}$; otherwise, the form of the relationship between species richness and energy will be scale invariant; that is, the relationship between energy and $\overline{D_\gamma}$ will always have the same form as the relationship between energy and $\overline{D_\alpha}$ because any contribution of D_β to $\overline{D_\gamma}$ will be independent of energy (fig. 1B; Scheiner et al. 2000).

A linear relationship between energy and D_β, as described above, may radically transform a species-energy relationship that is not linear at an explicitly local scale of analysis (across communities) to one that is strongly linear at regional scales. This phenomenon may be prominent in freshwater assemblages (Chase and Leibold 2002), perhaps because of their dispersal-limited nature (Magnuson et al. 1998), which could reinforce the link between energy and $\overline{D_\beta}$ (Chase and Ryberg 2004). Here we undertake the first large-scale investigation of scale dependence in the relationship between species richness and energy in a group of freshwater species, specifically, fishes in 7,885 lake sites distributed over an area of approximately 800,000 km^2 in the province of Ontario (see app. A in the online edition of the *American Naturalist*). We use a large database of occurrence records for these species, derived from lake surveys, to test the simple model of scale dependence described above by examining the relationship between species richness and energy at a local (lake) scale of analysis and at two successively larger regional (watershed) scales. Our investigations are facilitated by the discrete nature of lake fish communities and by the large size of the data set that we analyze.

We use potential evapotranspiration (PET), which is most directly a measure of thermal energy, as our energy metric because a preliminary analysis of the data showed that fishes in the sampled range respond strongly to PET (a fuller explanation and justification for our use of this metric can be found in app. B in the online edition of the *American Naturalist*). We should note that species richness can be related to two general types of energy (Currie et al. 2004; Clarke and Gaston 2006): (1) "energy" can refer to resource availability (Wright 1983), in which case it is measured as productivity or some index thereof; and (2) it can refer to thermal energy (e.g., Turner et al. 1988), often measured as temperature or PET. In fact, PET will likely affect lakes in terms of both resource availability (through a general correlation with lake productivity) and
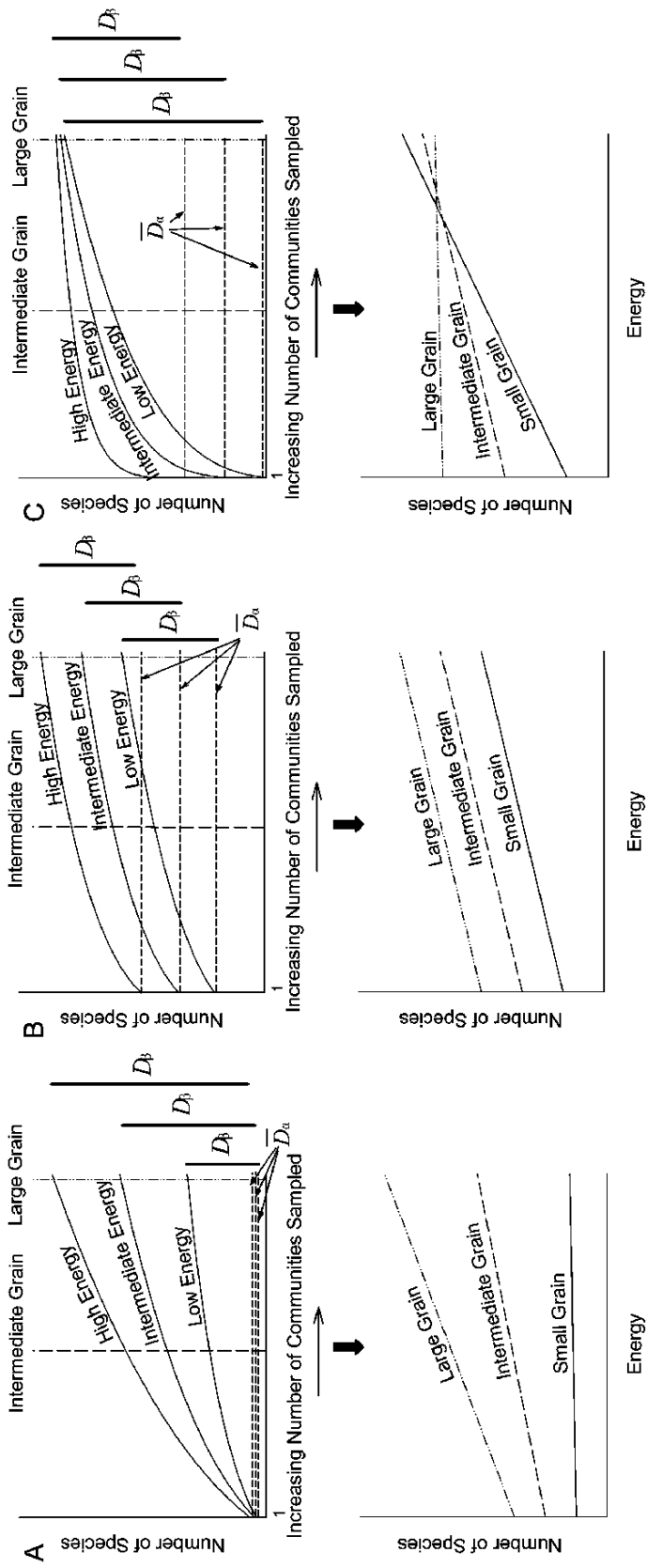
Figure 1: A model for scale dependence in the relationship between species richness and energy. *A*, Take, for simplicity, three regions that differ in energy by equal increments. The species richness of the first community sampled in each, assuming that it is typical, will account for its alpha diversity (in the example depicted, there is little difference in the alpha diversity of regions of different energy, suggestive of a weak relationship between energy and species richness at the scale of individual communities). A linear relationship between energy and the beta diversity component of regional richness (indicated by the vertical lines on the right) would arise if the rate of species accumulation differs between regions of different energy in the manner depicted as communities are sampled in greater numbers. This produces a positive and linear gradient in species richness across regions of increasing energy. Any factor that would increase the divergence of species accumulation curves, such as increasing the grain size of an analysis, would increase the slope of the species-energy relationship, as indicated in the bottom plot. (It will, of course, not strictly be true that the species accumulation curve of a region is a simple extension of that of a smaller region nested within it or that alpha diversity will remain identical as the size of regions is increased; increasing the size of regions will, however, extend the divergence of species accumulation curves, and it is this divergence that is responsible for the increasingly linear character of the species-energy relationship.) *B*, In cases in which species accumulate at the same rate across different levels of energy (i.e., there is no relationship between energy and beta diversity, as indicated on the right), the species-energy relationship will be scale invariant. *C*, In cases in which energy is positively related to the rate at which species accumulate at low levels of accumulation and negatively related to this rate at high levels of accumulation—reflecting a generally negative relationship between energy and beta diversity—the species-energy relationship can be less positive at large grains than small grains.

aspects of the thermal habitat (affecting, for example, temperatures, oxygen concentrations, and growing-season lengths; Kalff 2002), and its consequences for fishes in the sampled range may reflect a mixture of trophic and physiological responses (Matthews 1998; Jackson et al. 2001). Which of these is most important is not of major concern from the standpoint of the analyses presented here, as it is not our goal to contribute to debates concerning the ultimate cause of species-energy relationships. Rather, we are asking another fundamental question, as developed in figure 1: in what ways must energy structure species' distributions in order to elicit a scale-dependent response of species richness to energy?

Methods

Fish species distribution data come from an electronic database maintained by the Ontario Ministry of Natural Resources (OMNR), the Ontario Fish Distribution Database (OFDD), which provides approximately 160,000 records of occurrence indicating the collection of species from particular locations, with geographic coordinates, in most areas of the province (there is an absence of data from northern areas; fig. A1A). These records date from 1913 to the present, but 82% of the records have accumulated since 1968. Mandrak and Crossman (1992a) describe the history of the database to 1987; sampling methodology is described by Goodchilde and Gale (1982). We use the species records from lakes to examine the relationship between energy and species richness at a local grain (across lakes) and at successively larger regional (watershed) grains. The lakes that we analyze are inland lakes (they do not include the very large Great Lakes). In addition, we excluded two enormous inland lakes from our analyses—Lake of the Woods and Nipigon—because we are testing a model of scale dependence based on the accumulation of communities within regions (fig. 1), and these lakes are large enough to be considered regions in themselves. The lakes that we analyze have a mean area of 4.23 km² and a maximum area of 1,400 km². We analyze data from a total of 7,885 lake sites that include, collectively, 107 fish species (app. C in the online edition of the *American Naturalist*), a subset of the 153 species, excluding hybrids, recorded in the OFDD.

Watersheds are regions drained by major streams and rivers and are defined at arbitrary points along these watercourses or from one point to another. Ontario officially designates a set of "tertiary" watersheds nested within larger "secondary" watersheds (fig. A1B), which, for our purposes, represent regional grains of successively larger size; we do not analyze "primary" watersheds because there are only three of these. Secondary watersheds have, on average, five times the area of tertiary watersheds, although

there is variation in area at each of the three spatial grains that we analyze (fig. D1 in the online edition of the *American Naturalist*). We use watersheds rather than equal-area grid cells as our regional units because this removes the influence of catchment boundaries for differences in species turnover (and we wish to isolate the role of energy in this regard; fig. 1). Moreover, regions of equal area will differ greatly in water area, which may be a considerably more important aspect of regional area from the standpoint of fishes. In terms of the conceptual model we evaluate (fig. 1), regions are considered to be groups of communities, with regions of the smaller scale being nested within those of the larger. The areas in which the communities are distributed—and the areas of the communities themselves—can, of course, have important consequences, and we evaluate this below, controlling for within-scale area effects when necessary.

The OFDD is known to have certain biases with respect to sampling; in particular, sport fishes are overrepresented in the database, while small-bodied species, particularly cyprinids, are underrepresented (Minns 1986). In addition, lake surveys have been conducted over many years with the goal of providing a general characterization of local assemblages, and they do not provide quantitative standardization of sampling effort. For these reasons, the data are most appropriate for investigating regional-scale patterns, and although we investigate the species-energy relationship at the local scale (among lakes), our data will not estimate the relationship with a great deal of precision at this scale, and our conclusions are based, in part, on other studies (see "Discussion"). We note, however, that the model we evaluate (fig. 1) is explicitly one of how species-energy relationships can be transformed at increasing regional scales, and it makes no assumptions about the nature of the relationship at the local scale.

Our PET data come from climate averages for the period 1961–1990 (Centre for Land and Biological Resources Research 1997). These data are derived by applying gridded surface interpolation methods to climate station measurements and assigning area-weighted average values of these estimates to Soil Landscapes of Canada (SLC) "ecodistricts," which are regions characterized by homogeneous biophysical conditions (Centre for Land and Biological Resources Research 1996). There are 87 of these ecodistricts in the province of Ontario, with an average area of approximately 11,000 km². The sampled lakes (fig. A1A) fall within 70 of these ecodistricts; thus, PET estimates have 70 discrete values among lakes. Annual PET was estimated for each SLC ecodistrict from climate variables with the Thornthwaite method (Thornthwaite and Mather 1957). A geographic information system (GIS) map of ecodistricts was used to assign these PET estimates

to individual lakes. At regional scales, PET was computed as the mean PET of sampled lakes within watersheds.

At the local (lake) scale, species richness was computed as the number of species recorded in each lake. At the two larger (watershed) scales, we were interested in examining the effect of increasing the number of surveyed lakes within regions (fig. 1), and therefore, we used sample-based rarefaction to estimate species richness for different numbers of lakes. The EstimateS 7.5 package (Colwell 2005) was used to obtain species accumulation curves for each watershed, and the species richness of each tertiary watershed was estimated as the mean richness, from 500 random samples (sampling with replacement), for 10 lakes, 20 lakes, 30 lakes, and so on, up to 100 lakes. At the secondary-watershed scale, we estimated species richness for 49, 100, 164, 219, 249, 286, 345, 388, 410, and 434 lakes. In the case of secondary watersheds, these numbers were chosen to yield the same mean density of sampled lakes at this larger scale. For example, a sample of 10 lakes from each tertiary watershed yields a mean density of 1.35×10^{-5} lakes/ha across watersheds. An identical density is achieved across secondary watersheds if 49 lakes are sampled. Similarly, a sample of 20 lakes from each tertiary watershed corresponds to a sample of 100 lakes from each secondary watershed. We follow this procedure because it allows us to evaluate the effect of increasing the number of communities sampled within regions for the slope and strength of the species-energy relationship (fig. 1) while also providing 10 cross-scale comparisons in which sample coverage is held constant (which is the usual way that relationships with species richness are compared across scales) while the number of samples is varied, which would reveal an interaction between the number of samples and the scale effect. In increasing the number of sampled lakes in watersheds, there is a reduction in sample size: for example, 95 tertiary watersheds have at least 10 surveyed lakes, but only 26 of these have at least 100 lakes; our results are sufficiently clear, however, that this is not of great concern.

As noted above, there is variation in area within each of the three scales we analyze, which could confound measured species-energy relationships. We investigated the importance of this variation by examining the relationship between species richness and lake area or, at watershed scales, three different regional measures of area: mean lake area, total lake area (the summed area of surveyed lakes), and watershed area. Lake area data were provided in another electronic database maintained by the OMNR, the Lake Inventory Database (LINV). Watershed areas were estimated from a projected GIS map using ArcGIS (Environmental Systems Research Institute 2004).

Relationships with species richness can be complicated by historical patterns of dispersal. We therefore examined, at each scale, the relationship between species richness and latitude, a variable that captures the general north-south orientation of the historical dispersal gradient for fishes in the sampled range, which have assumed their present distributions by migrating, primarily from the south, since the last (Wisconsinan) glacial advance (Crossman and McAllister 1986; Mandrak and Crossman 1992b). Latitude data for lakes were provided in the OFDD. The latitude of watersheds was computed as the mean latitude of surveyed lakes.

Our analyses are potentially influenced by contagious biotic processes that would cause spatial autocorrelation in the distribution of species richness (Legendre 1993), and we investigated this using partial Mantel tests (Smouse et al. 1986). The test for whether there is a significant amount of spatially structured variation in species richness that cannot be explained by PET is a partial Mantel test relating a matrix of pairwise differences in species richness to a matrix of geographic distances, after the removal of shared variation between the geographic distance matrix and a matrix of pairwise differences in PET. Mantel tests, based on 1,000 permutations, were performed using the "ecodist" package for R (Goslee and Urban 2006).

Scale dependence, as modeled in figure 1A, is based on a divergence of species accumulation curves among regions of different energy. We examined this directly by computing "average" species accumulation curves for watersheds falling within different energy categories. The shapes of these curves are determined by distributions of relative site occupancy or, less directly, abundance (Lande 2000; Thompson and Withers 2003), and we also examined how these distributions differ with respect to regional energy.

Scale dependence in the relationship between species richness and energy has been linked to two additional patterns that we investigate. Chase and Leibold (2002) suggest that it reflects an association between energy and pairwise compositional dissimilarity between samples that may cause species to accumulate relatively quickly in regions of high energy (fig. 1A) and may reflect the influence of energy on environmental heterogeneity. We evaluated this by relating the PET of watersheds to their mean proportion of unshared species (i.e., the mean of 1 − Jaccard's index) from all pairwise comparisons between lakes. (Note that the term "beta diversity" can refer to such measures of pairwise compositional dissimilarity but is here reserved for D_β). Bonn et al. (2004) suggest that energy will influence beta diversity if it structures species' distributions in such a way that they exhibit a nested subset pattern of regional occupancy; a perfectly nested subset pattern would be one in which species found in a region of a given level of energy are also found in all higher-energy regions. This was assessed (Wright and Reeves

1992) at the scale of tertiary watersheds—this being our regional scale of highest resolution—by ranking watersheds from highest to lowest PET and, for each species, computing the probability that watersheds in which it is found are not of higher rank than those in which it is not, using one-tailed Mann-Whitney *U*-tests, and then combining these independent tests using Fisher's method (Sokal and Rohlf 1995).

Relationships between species richness and other variables (area, latitude, and PET) were generally analyzed using ordinary least squares (model I) regression. At the scale of lakes, relationships were sometimes measured using a generalized linear model, assuming Poisson errors and a logarithmic link function, in R (R Development Core Team 2005), when we were unable to normalize the distribution of residual errors.

Results

Importance of Area and Latitude

As noted above, the importance of within-scale variation in area (summarized in fig. D1) and the potentially confounding effects of latitude must be assessed before richness-PET relationships at different scales can be evaluated. Log$_{10}$-transformed lake area is strongly related to the log$_{10}$-transformed species richness of lakes ($F = 3,734.87$, df $= 1, 7,883$, $r^2 = 0.321$, $P < .001$). The species richness of lakes is also significantly related to latitude (as analyzed by a generalized linear model: likelihood ratio $\chi^2 = 584.602$, df $= 1$, $P < .0001$); however, latitude explains a tiny amount of deviance in the species richness of lakes (3.2%), and for this reason, we do not consider its influence further at the lake scale. We also investigated the importance of elevation and several lake morphometric and chemical variables at this scale (app. E in the online edition of the *American Naturalist*; these variables were provided in the LINV database; [see "Methods"]), but none of these variables accounted for much variation in the species richness of lakes—the most important were other measures of lake size (e.g., depth, perimeter), which are strongly correlated with lake area—and for this reason, we do not consider them further.

Results of the analysis of the importance of different measures of area for watershed species richness are provided in appendix D in the online edition of the *American Naturalist*. Measures of area are only occasionally significantly related to species richness at these scales (table D1) and only when richness is estimated for a small number of lakes. Moreover, the central prediction of the model under evaluation (see the introduction to this article) is that the richness-PET relationship should become stronger and steeper at increasing scales. In order for area to con-

tribute to such a pattern, it would have to co-vary positively with watershed PET and increasingly so at increasing scales. However, area does not co-vary with PET in this way (fig. D2), and we therefore do not control for its variation when measuring the richness-PET relationship across tertiary or secondary watersheds.

At watershed scales, species richness is usually significantly (negatively) related to latitude. Stepwise multiple-regression analyses relating species richness, measured for different numbers of lakes at both tertiary- and secondary-watershed scales, to latitude and PET (probability of *F* to enter: ≤0.05; probability of *F* to remove: ≥0.1) always resulted in PET being entered into the model first, while latitude was usually not entered (when it was entered, both variables were retained; maximum variance inflation factor for latitude: 3.7). This indicates that PET is a more important predictor of species richness than is latitude. However, because of the strong correlation between latitude and PET ($r = -0.83$ and -0.89 for tertiary and secondary watersheds, respectively; $P < .001$ in both cases), we examine the relationship of both to watershed species richness below; patterns that are unique to PET cannot be attributed to the dispersal-related effects of latitude.

To summarize, we take area into account when assessing the richness-PET relationship across lakes but do not otherwise consider area or latitude when measuring richness-PET relationships at different scales. However, we also examine how the richness-PET relationship differs from the richness-latitude relationship.

Scale Dependence of the Richness-PET Relationship

To partition the effects of lake area and energy for species richness at the lake scale, we ran a generalized linear model on the data. We tested the model species richness $= a + b(\log_{10} \text{area}) + c(\text{PET}) + d(\text{PET})^2$. The quadratic term was included in order to identify a unimodal relationship between species richness and energy, often observed when richness is related to the productivity of water bodies (Waide et al. 1999). All model coefficients were found to be significant (likelihood ratio tests: $\chi^2 = 7,218.14$, 59.04, and 78.61 (df $= 1$) for *b*, *c*, and *d*, respectively; $P < .001$ in all cases), but in the case of the PET terms, this is primarily attributable to the large sample size, and lake area accounts for virtually all of the explained deviance, which is 34.56% and 40.15% for lake area and the complete model, respectively, with terms entered sequentially in the order given by the above equation. Thus, area is the most important predictor of species richness among lakes, and PET has little additional explanatory power at this scale (fig. 2).

Across tertiary and secondary watersheds, species richness is strongly and linearly related to PET, and PET ex-

plains progressively more variation in richness as the number of lakes for which it is estimated increases (fig. 3). In addition, the slope of the richness-PET relationship rises as the number of sampled lakes increases (fig. 4) and is always significantly steeper at the larger (secondary-watershed) scale (fig. 4A), except when sample density is very low. Moreover, the effect of scale (difference in the slope between scales) increases as sample density increases (fig. 4A). All of these effects are due to the influence of PET on the D_β component of regional richness (fig. 3); PET is not related to the $\overline{D_\alpha}$ component (i.e., mean lake richness) at either the tertiary- or the secondary-watershed scale ($F = 0.03$, df $= 1, 93$, $r^2 = 0.00$, $P = .857$, and $F = 0.53$, df $= 1, 24$, $r^2 = 0.02$, $P = .47$, respectively). There is no effect of scale if the number of samples in watersheds, rather than their density, is held constant (fig. 4B).

Spatial autocorrelation in species richness that is unrelated to the spatial dependence of richness on PET does not appear to have contributed to any of the patterns noted above (table F1; fig. F1 in the online edition of the *American Naturalist*). The patterns are predicted if energy has a linear effect on D_β, which, in turn, reflects the influence of energy on species accumulation (fig. 1A); and watersheds of different energy exhibit species accumulation curves that diverge in the manner expected from our model (fig. 5A, 5B). Of note, the low-energy curves plateau at relatively low levels of accumulation. As would be expected, the underlying site occupancy distributions of watersheds of different energy are distinct (fig. 5C, 5D). Dominance-diversity curves from low-energy watersheds are short and steep, indicating high dominance (relatively few species account for a relatively large proportion of the total occurrences). Curves become longer and flatter, indicating greater evenness in the distribution of site occupancy, as energy increases.

There is a significant, although noisy, relationship between watershed PET and pairwise compositional dissimilarity among lakes (fig. 5E, 5F). Interestingly, however, compositional dissimilarity among lakes is not related to the species richness of watersheds; significance is most closely approached at the tertiary-watershed scale when richness is estimated for 10 lakes ($F = 2.45$, df $= 1, 93$, $r^2 = 0.026$, $P = .121$). In terms of the additive components of regional richness (eq. [1]), dissimilarity strongly predicts $\overline{D_\alpha}$ (mean lake richness): $F = 86.28$, df $= 1, 93$, $r^2 = 0.481$, $P < .001$ for tertiary watersheds; $F = 18.83$, df $= 1, 24$, $r^2 = 0.44$, $P < .001$ for secondary watersheds. This relationship is negative; that is, dissimilarity falls as the species richness of individual lakes rises. Given the importance of lake area for the species richness of lakes ("Importance of Area and Latitude"), it is not surprising, then, that the mean area of lakes strongly predicts their compositional dissimilarity (tertiary watersheds: $F =$

95.02, df $= 1, 93$, $r^2 = 0.505$, $P < .001$; secondary watersheds: $F = 60.30$, df $= 1, 24$, $r^2 = 0.715$, $P < .001$), with larger lakes yielding lower dissimilarities. Dissimilarity is generally unrelated to the D_β component of regional richness; for example, at the tertiary-watershed scale, it is significantly related to D_β when richness is estimated for 10 or 20 lakes (D_β being calculated by subtracting $\overline{D_\alpha}$ from these estimates; eq. [1]) but not for higher numbers of lakes (maximum $r^2 = 0.134$).

Species exhibit a nested subset pattern of regional occupancy ($\chi^2 = 693.74$, df $= 210$, $P < .001$; fig. 6). Associated patterns (Bonn et al. 2004) point to the generally greater geographic and ecological restriction of species found in high-energy regions; for example, there is a negative relationship between the PET of watersheds and the mean geographic range (number of occupied watersheds) and mean PET range (difference between the maximum and minimum PET of occupied watersheds) of the species that they contain ($F = 229.35$, df $= 1, 93$, $r^2 = 0.708$, $P < .001$ and $F = 89.37$, df $= 1, 93$, $r^2 = 0.490$, $P < .001$, respectively). There is also a strong positive relationship between the number of watersheds occupied by species and their ($\log_{10}$) mean number of occurrences within occupied watersheds ($F = 326.46$, df $= 1, 105$, $r^2 = 0.757$, $P < .001$; fig. 6); that is, species with large ranges tend to be frequent wherever they are found, and vice versa.

The Richness-Latitude Relationship

The species richness–latitude relationship (summarized in app. G in the online edition of the *American Naturalist*) is generally significant when measured across watersheds, but the slope of this relationship does not show a general trend of becoming steeper as the number of lakes within watersheds increases and does not differ significantly between the tertiary- and secondary-watershed scales (fig. G1). As would be predicted, given this lack of scale dependence, species accumulation curves for watersheds of different latitude do not diverge as strongly as they do among watersheds of different PET, and the influence of latitude on the evenness of site occupancy distributions is not as great (fig. G2). There is a strong tendency, however, for species dissimilarity among lakes to be greatest at low latitudes (fig. G2); indeed, latitude appears to have a considerably stronger influence on dissimilarity in species composition among lakes than does energy.

Discussion

In this study, we have investigated how energy influences spatial turnover in species composition in order to produce different relationships between species richness and energy at different scales of analysis (Scheiner et al. 2000; Chase
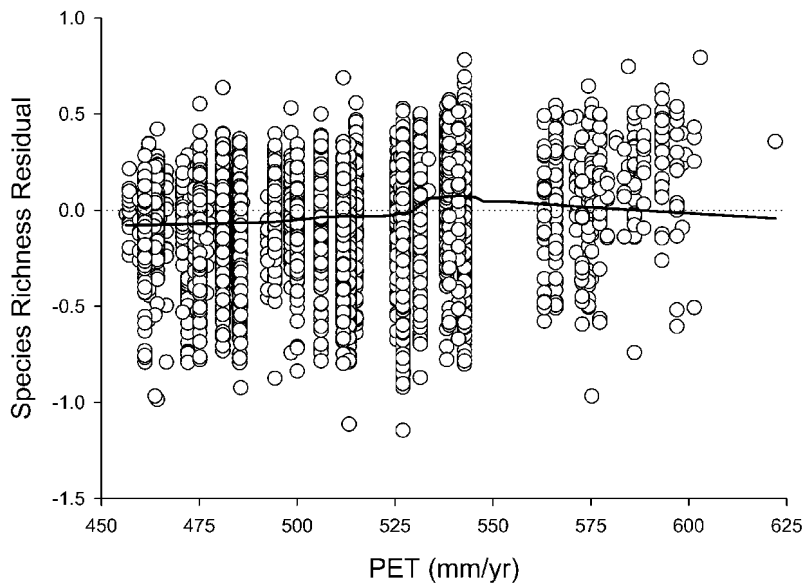
Figure 2: Scatterplot of fish species richness versus annual potential evapotranspiration (PET) at the lake scale. Species richness values are residuals from a regression of $\log_{10}$(species richness) on $\log_{10}$(lake area), in units of hectares (note: because of skewness in the distribution of these residuals, we do not fit a linear model to these data; rather, we analyze the relationship between species richness and PET at this scale using a generalized linear model, as described in the text). Gaps in the distribution of PET reflect the way in which PET estimates were obtained (see "Methods"). A LOWESS regression line indicates the overall trend in the data.

and Leibold 2002). A conceptual model (fig. 1*A*) has been described that accounts well for changes in the linear character of the richness-PET relationship as it is measured at increasing scales in a large number of freshwater fish assemblages. We briefly discuss the mechanisms that may underlie the influence of PET for the distributions of these fishes below; our main goal, however, has been to identify features of these distributions that generate scale dependency in the relationship between species richness and energy.

Our data show little evidence for a relationship between species richness and PET at the scale of individual lakes (fig. 2). When this relationship is examined at the spatial extent of Ontario, it is difficult to control for the many factors that could potentially mask the influence of energy at this scale. This consideration, along with sampling problems that have been noted ("Methods"), means that conclusions about the relationship across lakes must be informed by other studies in which the influence of energy could be more effectively isolated (e.g., Bachmann et al. 1996; Jeppesen et al. 2000). Such studies suggest that although energy is important for fish abundances, or "yields" (Downing et al. 1990; Jeppesen et al. 2000), there is no strong relationship with species richness; rather, lake surface area appears to be the chief correlate of the number of fish species at this scale (Barbour and Brown 1974), which may be because it is a surrogate for important aspects of habitat complexity (Tonn and Magnuson 1982). Although energy can influence habitat complexity (e.g., by increasing vegetation diversity) and does show some relationship with fish species number in certain contexts (Tonn and Magnuson 1982; Eadie and Keast 1983), the complexity of a lake, from the standpoint of fishes, appears to be more clearly a function of lake size than of energy.

This, of course, is not to say that energy is unimportant for the composition of local fish assemblages. This importance manifests itself as differences in the rate of sample-based species accumulation in regions of different PET (fig. 5*A*, 5*B*), which link the energy of lakes to regional variation in species richness. Differences in the rates at which species are accumulated when increasing numbers of communities are counted reflect the influence of energy for beta diversity (fig. 1). In this study, we have drawn a parallel between the way that species accumulate when they are counted over greater numbers of communities and the way that they accumulate when the size of regions is increased (i.e., the scale of the analysis is increased; fig. 1). There are, of course, important differences in these two processes, and it is only the influence of energy for the latter (equivalent to a nested species-area curve) that corresponds strictly to scale dependence in the species-energy relationship. In both cases, however, the accumulation of species is influenced by their distributions across sampled communities (Colwell and Coddington 1994; Rosenzweig 1995; He and Legendre 2002)

so that, for example, relatively rare species are sampled only after large numbers of samples have been taken into account. Scale-dependent change of the type that would increase the linear character of a species-energy relationship is the product of a divergence process (fig. 1*A*), and insofar as species respond to energy in a consistent way, the effect of increasing the scale of analysis would be to carry this process to higher levels of accumulation (the similarity of this divergence process across scales can be judged by comparing fig. 5*A* with fig. 5*B*).

The effects of both increasing the number of samples and increasing the scale of analysis are illustrated in figures 3 and 4. These results show that the relationship between PET and species richness is strong at both of the regional scales considered and becomes increasingly so as richness is estimated for larger numbers of surveyed lakes. In addition, as the number of lakes within regions increases, the slope of the richness-PET relationship rises steadily. Both of these trends are due to the influence of energy on the D_β component of regional richness (fig. 3), suggesting that factors related to species turnover among freshwater fish assemblages have an overriding importance in explaining richness patterns at large scales (see, e.g., Guégan et al. 1998). The trend for the slope to increase is best described by a positively decelerating curve, indicating that it will not continue ad infinitum; however, the trend remains strongly positive as the number of lakes within regions is taken to the limit that our data set will allow (fig. 4). As the density of lakes within watersheds increases, the effect of scale (difference in slope across scales) also increases (fig. 4*A*). This is because the number of samples is increased more quickly at the larger scale in holding sample density constant, emphasizing the importance of the divergence process illustrated in figure 1*A* in generating the scale effect. If the richness-PET relationship is measured for the same number of lakes across tertiary and secondary watersheds, the slope is not higher when measured across the larger watersheds (fig. 4*B*), underscoring this point.

Understanding scale dependence in the richness-PET relationship would appear, then, to be a matter of understanding why sample-based species accumulation curves diverge for regions of different energy. This divergence is attributable to the high dominance of relative site occu-
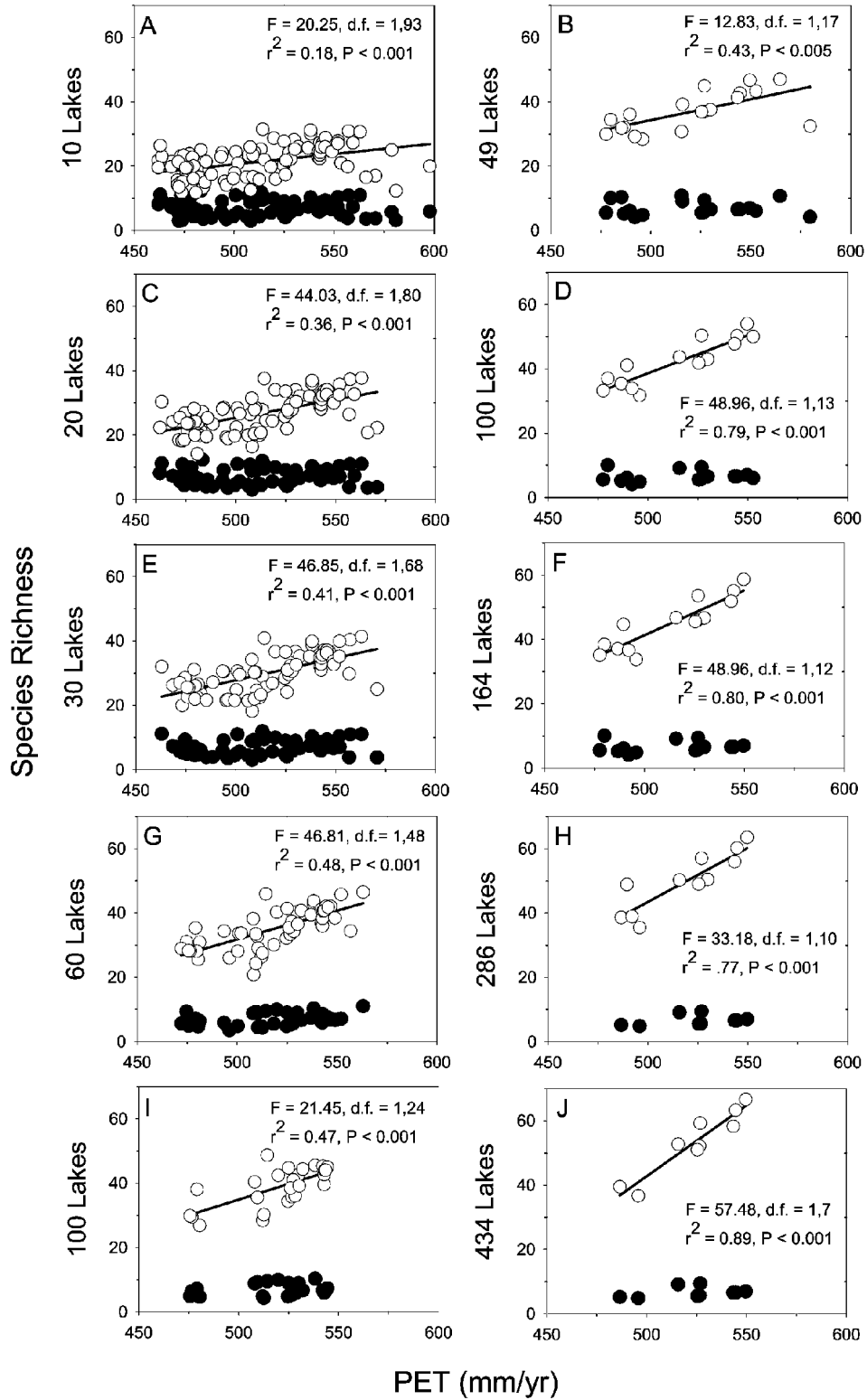
pancy in low-energy regions (fig. 5*C*, 5*D*), which causes species accumulation curves in these regions to plateau quickly (fig. 5*A*, 5*B*). Higher-energy regions are characterized by more even distributions of site occupancy; that is, relatively infrequent species continue to be added at high levels of accumulation. We would predict, therefore, that a tendency for species-energy relationships to become more positively linear at increasing spatial grains will generally be associated with a relation between energy and the evenness of site occupancy distributions and, less directly, with evenness in distributions of relative abundance. Richness is not necessarily linked to evenness (Ma 2005; Wilsey et al. 2005), and such an association may indicate the operation of distinctly nonneutral (ecological) processes (Bell 2000; Stirling and Wilsey 2001). It is important to note that a positive association between richness and evenness along an energy gradient will not necessarily produce the pattern observed here. For example, if the effect of high energy is to make site occupancy distributions extremely even, so that species accumulation curves plateau quickly, then curves for regions of different energy may converge rather than diverge (fig. 1*C*; Lande 2000), potentially producing a less positive relationship at large scales than at small; Storch et al. (2005) provide evidence for this type of scale dependency in birds. There is thus a distinction to be made between a transition—in association with increasing energy—from high dominance to moderate evenness and one from moderate to very high evenness. The first type of transition produces a positive effect of energy on beta diversity (D_β; fig. 1*A*), while the second may produce a generally negative effect (fig. 1*C*).

Although there is a significant association between PET and pairwise compositional dissimilarity among lakes, measured as $1 -$ Jaccard's index (fig. 5*E*, 5*F*), dissimilarity is not, in turn, strongly linked to the D_β component of regional richness (see "Results"), although it is the influence of energy on D_β that is responsible for the scale dependence that we observe (fig. 3). Species dissimilarity among samples, therefore, does not seem to be very important for understanding the phenomenon under investigation (see also Harrison et al. 2006). Underscoring this point, dissimilarity co-varies quite strongly with latitude, and yet there is no difference in the richness-latitude relationship across regional scales (app. G). Dissimilarity is

Figure 3: Relationships between potential evapotranspiration (PET) and the species richness of tertiary and secondary watersheds (*open circles*). Species richness is estimated for the number of lakes indicated by the *Y*-axis labels, and the relationships are based on increasing numbers of lakes as one proceeds down each column; trends of increasing slope and explained variance are evident. Rows represent cross-scale comparisons. Thus A–B, C–D, etc., indicate the trend of increasing slope and explained variance as a consequence of increasing the scale of analysis (holding sample density constant; see "Methods"). Filled circles show the relationship between PET and the alpha diversity ($\overline{D}_\alpha$) component of species richness (i.e., mean lake richness). The differences in the responses of alpha diversity and total species richness are due to the influence of PET on beta diversity (D_β), which is clearly responsible for the illustrated trends in species richness.

Species Richness

A — 10 Lakes
F = 20.25, d.f. = 1,93
$r^2 = 0.18$, P < 0.001

B — 49 Lakes
F = 12.83, d.f. = 1,17
$r^2 = 0.43$, P < 0.005

C — 20 Lakes
F = 44.03, d.f. = 1,80
$r^2 = 0.36$, P < 0.001

D — 100 Lakes
F = 48.96, d.f. = 1,13
$r^2 = 0.79$, P < 0.001

E — 30 Lakes
F = 46.85, d.f. = 1,68
$r^2 = 0.41$, P < 0.001

F — 164 Lakes
F = 48.96, d.f. = 1,12
$r^2 = 0.80$, P < 0.001

G — 60 Lakes
F = 46.81, d.f.= 1,48
$r^2 = 0.48$, P < 0.001

H — 286 Lakes
F = 33.18, d.f. = 1,10
$r^2 = .77$, P < 0.001

I — 100 Lakes
F = 21.45, d.f. = 1,24
$r^2 = 0.47$, P < 0.001

J — 434 Lakes
F = 57.48, d.f. = 1,7
$r^2 = 0.89$, P < 0.001

PET (mm/yr)
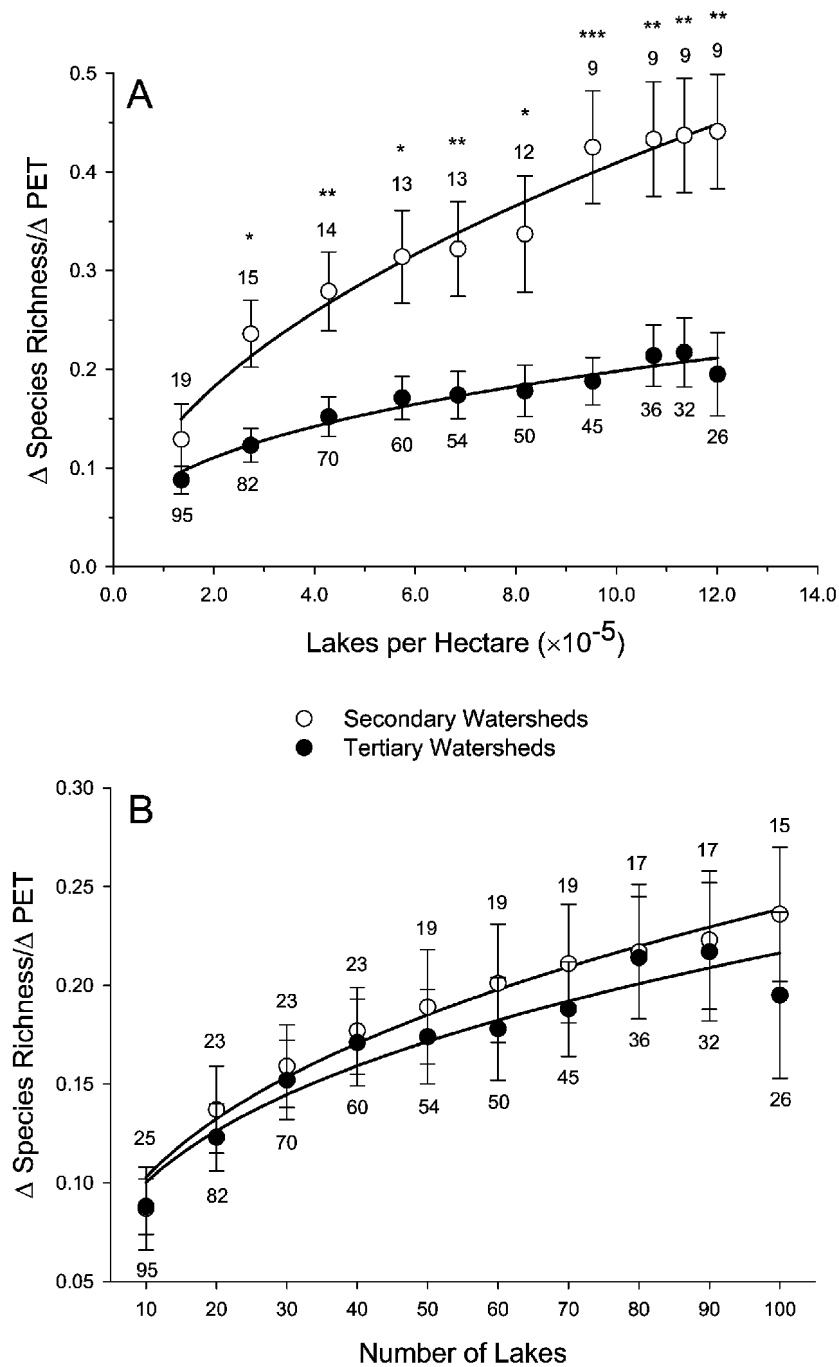
Figure 4: *A*, Slopes from regressions of watershed species richness on watershed potential evapotranspiration (PET) versus the mean density at which lakes are sampled within watersheds. Labels indicate the sample sizes of the regressions, bars indicate standard errors of the slopes, and fitted power relationships illustrate trends in the slope parameter (tertiary watersheds: $r^2 = 0.95$; secondary watersheds: $r^2 = 0.97$). At all lake densities except the lowest, the slope is significantly steeper at the larger secondary watershed scale, as determined by a *t*-test (one asterisk indicates $P < .01$; two asterisks indicate $P < .005$; three asterisks indicate $P < .001$). *B*, Comparison of slopes from regressions of watershed species richness on PET when species richness is estimated for the same number of lakes in tertiary and secondary watersheds (i.e., when sample number, rather than sample coverage, is standardized). In this case, the trend for the slope to increase is the same, and measuring the richness-PET relationship across the larger secondary watersheds does not yield significantly higher slopes.
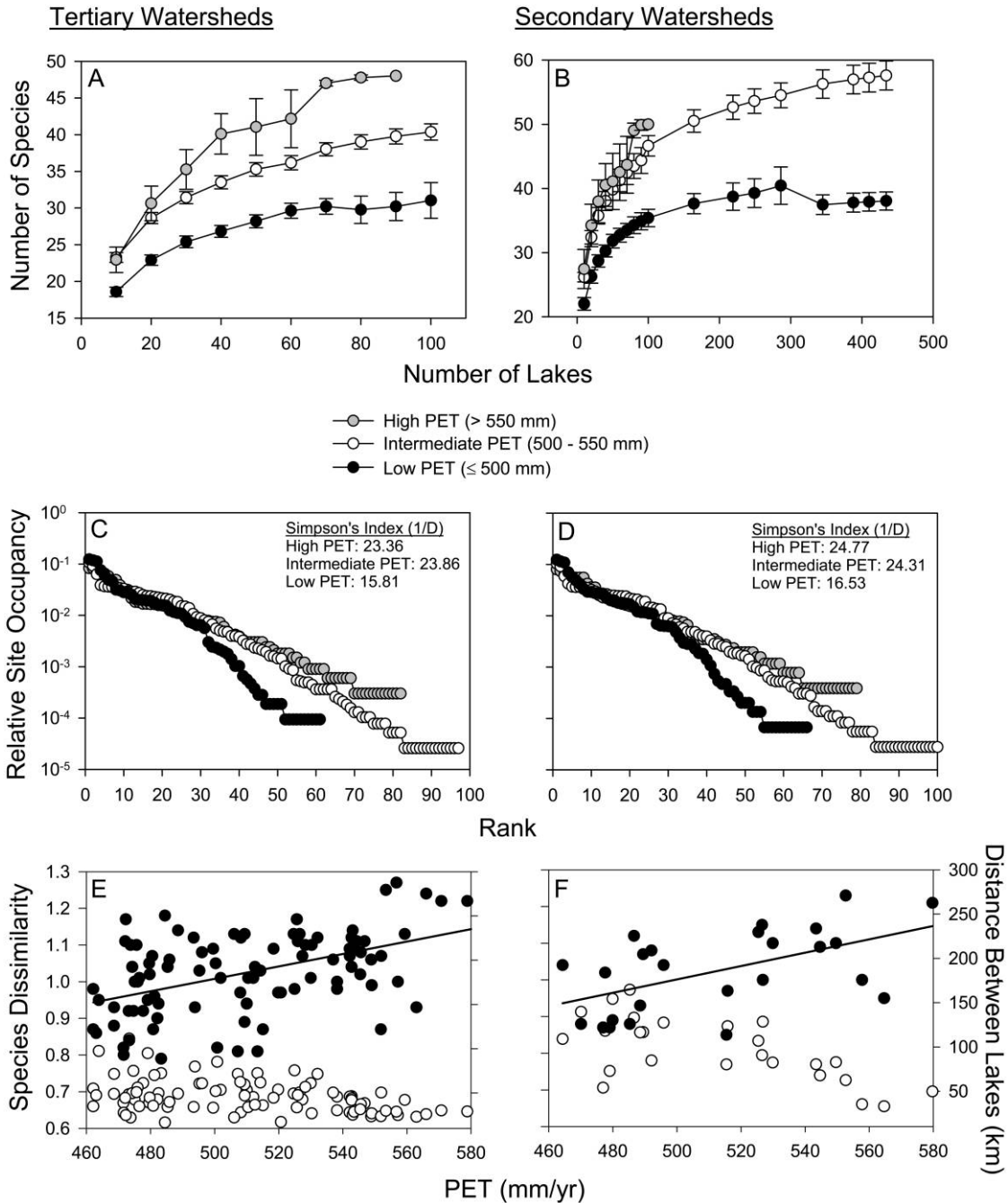
Figure 5: Average species accumulation curves for tertiary watersheds (*A*) and secondary watersheds (*B*) falling within different energy classes. *C*, *D*, Rank occupancy distributions for species falling within each energy class, in the form of dominance-diversity curves. Simpson's index (a measure of evenness) is indicated for each energy class; the higher this index, the greater the probability that two records randomly sampled from these distributions will be for different species. *E*, *F*, Relationships between the potential evapotranspiration (PET) of watersheds with at least 10 surveyed lakes and mean pairwise species dissimilarity (*filled circles, left axes*). Dissimilarity between lakes is computed as $1 -$ Jaccard's index and is arcsine-of-square-root transformed. Open circles indicate the mean pairwise geographic distance between lakes (*right axes*). Species dissimilarity is positively related to PET (tertiary watersheds: $F = 31.16$, df $= 1, 93$, $r^2 = 0.251$, $P < .001$; secondary watersheds: $F = 9.96$, df $= 1, 23$, $r^2 = 0.302$, $P = .004$) despite the generally smaller distance between surveyed lakes in high-PET watersheds.
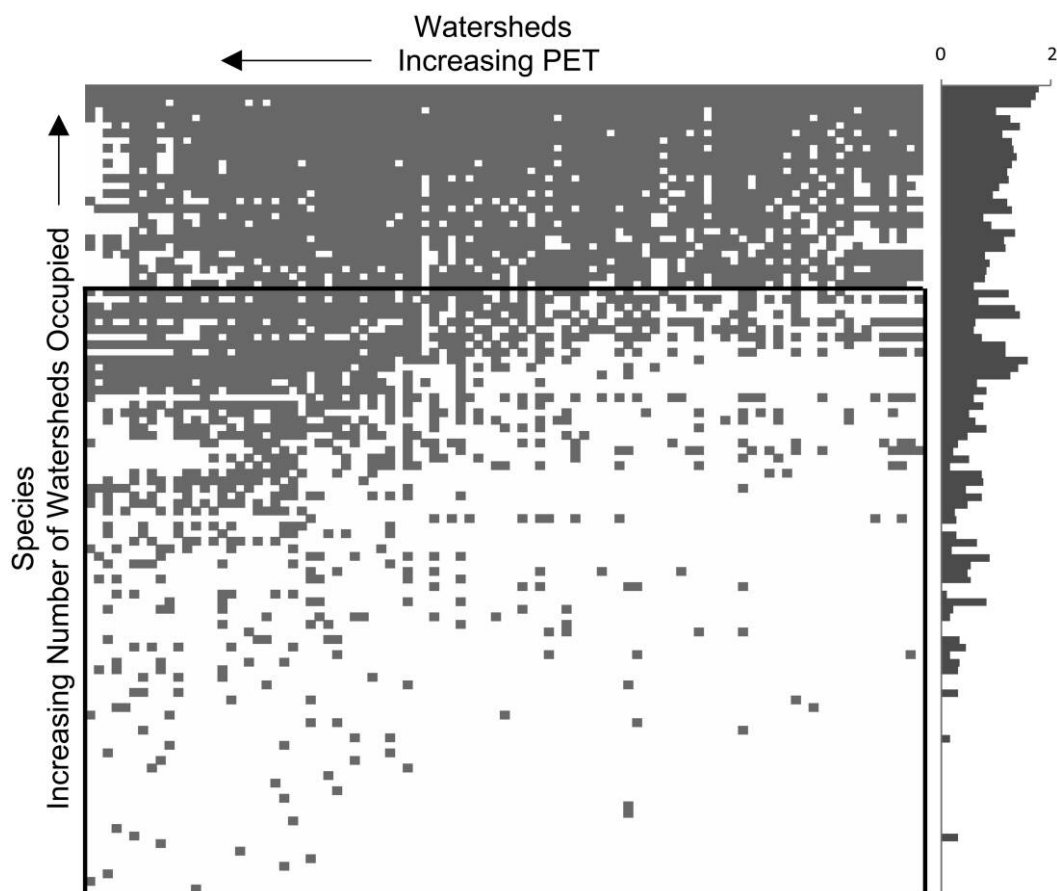
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Figure 6: Species-by-sites matrix (sites are tertiary watersheds), with species presences indicated by gray squares. Species (rows) are sorted by number of presences (ties are sorted at random) so that species occupying the most watersheds represent the highest rows. Watersheds (columns) are sorted by the mean potential evapotranspiration (PET) of their surveyed lakes. The overall pattern indicates that some species, accounting for the top rows, have generalist distributions (see app. B in the online edition of the *American Naturalist* for information on the identities of these species). In addition, there is a tendency, evident within the outlined region, for species found in fewer and fewer watersheds to be increasingly restricted to the highest-energy regions. Thus, high-PET watersheds have relatively large numbers of species with smaller geographic ranges, on average, than those in low-PET watersheds and a tendency to be found in a relatively narrow range of energetic conditions. A less nested pattern would be evident if all species had similar geographic ranges. The bar graph on the right indicates ($\log_{10}$) average frequency of occurrence of each species within occupied watersheds.

more strongly related to the $\overline{D}_\alpha$ component of regional richness than to D_β, indicating that different measures of "species turnover"—Jaccard's index and D_β in this case—need not correspond in any straightforward manner (Clarke and Lidgard 2000; Koleff et al. 2003).

The distribution of fishes within the surveyed range exhibits a nested subset pattern of regional occupancy (fig. 6). Such patterns may have a variety of causes (Wright et al. 1998; McAbendroth et al. 2005), but the most plausible candidates would be (1) species differ in their ability to colonize low-PET watersheds (which tend to be most distant from their glacial refuges), so that many species are found in high-PET watersheds but only the best dispersers are found in all; and (2) only incrementally smaller nested

subsets of these species can survive in watersheds of progressively lower PET, so that the lowest-PET watersheds have the most cosmopolitan species. The first mechanism suggests that species accounting for the top rows in figure 6 are inherently the best dispersers, while the second suggests that they are generalists with respect to conditions within the surveyed range (see app. C for the identities of these species). There is, in fact, no obvious reason to distinguish the species above the boxed region in figure 6 on the basis of their inherent capacity to disperse, although one species within the boxed region, the American eel, *Anguilla rostrata*, is clearly prevented from straying very far from Great Lakes by its catadromous life history.

As noted above ("Results"), there is a strong positive

association between the number of watersheds occupied by species and the number of their occurrences within occupied watersheds (fig. 6); this association seems to link the nested subset pattern to the trend for the richness-PET relationship to become strongly linear at regional scales (figs. 1*A*, 3, 4) because it indicates that high-energy regions have a mix of frequent and infrequent species, while species-poor low-energy regions are dominated by frequent ones. Hypotheses that could account for these relationships (Bell 1997; Guégan et al. 1998; Bonn et al. 2004; Evans et al. 2005, 2006) invoke the generally greater heterogeneity and resource availability of high-energy regions and their attendant ability to sustain rare species, which may be ecological specialists adapted to uncommon conditions within the surveyed range. There are, indeed, species accounting for the lower rows in figure 6 that have well-known associations with conditions related to PET, such as tolerance for very high water temperatures (Scott and Crossman 1998), which would be uncommon in Ontario. It may also be the case that many of these species are not adapted to the cold temperatures, short growing seasons, and long months of ice cover that characterize low-energy regions (e.g., King et al. 1999; Fang and Stefan 2000), so that their restricted distributions primarily reveal their physiological tolerances for aspects of the thermal habitat (Currie et al. 2004). Distributions within the surveyed range would then ultimately reflect processes of evolutionary diversification that took place, for many of these species, in warmer climates (Crossman and McAllister 1986; Mittelbach et al. 2007).

A question arises as to the extent to which our results may have been affected by the stocking of fishes. Heavily stocked species tend to be frequent ones, and the effect of stocking would be to increase their frequency further, likely increasing dominance, which could be reinforced by negative interactions of commonly stocked species with others (Vander Zanden et al. 2004). On balance, stocking would have the greatest effect on high-PET watersheds, owing to their greater accessibility. However, we have shown that scale dependence of species-energy relationships is the product of a positive association between energy and the evenness of occupancy distributions. As the effect of stocking on the evenness of high-energy regions is likely negative, stocking could not have reinforced the patterns of scale dependence that we have observed.

Conclusions

The species richness–PET relationship is extremely scale dependent in fishes in postglacial lakes. This scale dependence results from the influence of PET on beta diversity (fig. 1), which, in turn, results from its influence on the evenness of site occupancy distributions. This suggests that when evaluating species-energy relationships at regional scales, one should examine patterns of site occupancy (or abundance, if that is the nature of the data) at different levels of energy. If energy is strongly tied to occupancy or abundance, one should suspect that the relationships being measured depend on the scale of measurement; understanding this scale dependence is a matter of understanding how energy influences the occupancy or abundance patterns of species.

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