

## WHAT IS THE OBSERVED RELATIONSHIP BETWEEN SPECIES RICHNESS AND PRODUCTIVITY? COMMENT

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The form of the species richness–productivity relationship (SRPR) remains central to our understanding of species diversity controls. Mittelbach et al. (2001) built on Waide et al. (1999) to provide the first large-scale, formal meta-analysis of the SRPR, based on 257 data sets from 171 publications. Their aim was to classify each relationship as negative, positive, U shaped, or hump shaped, in the context of recent suggestions that the general form of the SRPR is hump shaped (e.g., Rosenzweig and Sandlin 1997, Huston 2001). The central findings of the meta-analysis are that there is no single *general* pattern, and that patterns are scale and taxon dependent. We concur with these conclusions (also see Chase and Leibold 2002), and applaud the intent of their analysis. However, we raise concerns over three issues: (1) the treatment of scale; (2) the treatment of surrogate productivity variables; and (3) potential bias in the statistical procedures followed in the meta-analysis.

The subset of studies we examine in detail is of tree data sets, classed by Mittelbach et al. (2001) as “regional” or “continental-global” in scale. A priori, we expect a positive SRPR to be evident for trees at the macro-scale (see O’Brien et al. 1998, Whittaker et al. 2001). Such a relationship is consistent with our general understanding of geographical gradients of species richness in trees (Currie and Paquin 1987, O’Brien 1993, 1998) and of estimates of net primary productivity (NPP) variation across biomes (Lieth and Whittaker 1975, Esser 1998). Our reexamination was prompted by the (to us) unexpected degree to which

the meta-analysis reported humped, U-shaped, and negative SRPR for vascular plants (including several tree data sets) at coarse scales of analysis. At continental scales Mittelbach et al. (2001) found hump-shaped and positive SRPR to be co-dominant, while at regional scales (geographical scales smaller than continents), hump-shaped SRPR dominated, occurring in 41–45% of all studies. For tree-data sets at these scales, over half were classed as humped by Mittelbach et al. (2001: Appendix A).

### Scale

Two facets of geographical scale should be distinguished for present purposes. The first is the physical size (area, volume) of the units used to sample the biota, or at which the data are aggregated for analysis; this is the focal scale, or *grain* of the data (Palmer and White 1994). In illustration, a 1-m<sup>2</sup> vegetation plot presents a strictly limited physical space, in a particular microhabitat, constraining the number of individuals and the number of species from the pool that may be found in the plot (Oksanen 1996). In contrast, data collated from herbarium records using 10 000-km<sup>2</sup> grid cells will sample all available habitats, and will reveal the entire species pool. Patterns in richness at this focal scale (being macro-scale data) arise from the differential overlap of species ranges, while patterns in richness at the 1-m<sup>2</sup> scale (local or alpha scale) reveal the outcome of very local interactions within the range in response to competition, grazing, micro-habitat variation, etc. Fine-grain and coarse-grain richness data are thus phenomenologically different and should not be combined within a single analysis (Whittaker et al. 2001, and see Dungan et al. 2002, Koleff and Gaston 2002).

The second scale facet is the geographical extent over which the sample units are distributed, e.g., a hillside, the Amazon basin, or pan-tropically. Holding grain constant but increasing geographical extent will alter the range of values of independent environmental variables in the analysis, as well as likely sampling a greater array of biogeographical contexts. However, where a standard small plot size is used, the analysis will retain sensitivity to factors that vary at a fine scale. A priori, on phenomenological and statistical grounds, to be of use to sorting out factors controlling diversity, it is necessary to hold geographical scale, e.g. grain/focus constant. Holding extent constant is not so crucial, although it can be insightful to examine how the form of relationships alter as the range of values of environmental variables changes with increasing extent of study area.

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In the meta-analysis, results were organized according to taxa, and to the following two facets of scale: (1) “geographical scales,” subdivided into four levels, viz. local (<20 km), landscape (20–200 km), regional (200–400 km), and continental to global (>4000 km); (2) two forms of “ecological organization,” viz. within community types and across community types. Focusing on (1), it is apparent that Mittelbach et al. (2001) have organized their meta-analysis not by grain but by geographical extent. Analyses of coarse-grain (macro-scale) species-richness data are invariably undertaken across large geographical extents (e.g., Currie 1991), but the reverse does not apply (Waide et al. 1999): some studies are based on very small plots distributed across a large geographical extent (e.g., Phillips et al. 1994). For instance, in Mittelbach et al. (2001), the graph of continental-to-global scale studies of vascular plants (their Fig. 1) is based on 10 original analyses, including coarse-scale grid cells of ~50 600 to 96 000 km<sup>2</sup> (Currie and Paquin 1987), 0.1-ha data (e.g., Gentry 1988), 0.6 to 48 ha data (Phillips et al. 1994), and Wright’s (1983) analyses of islands varying in area from 1200 km<sup>2</sup> to 770 500 km<sup>2</sup>. These studies do qualify as ‘continental to global’ in their extent, but they vary across eight orders of magnitude from the local to the macro-scale in terms of grain. Direct comparison, or lumping of such studies is unsatisfactory, as it is likely to mix up different families of richness–productivity relationships in ways that may well not be detectable in subsequent statistical analysis (cf. He et al. 2002). A particular difficulty arises from the inclusion of Wright’s (1983) analysis, as its aim was to improve upon the statistical fit between log island area and log species number by using as the independent variable the interaction between a productivity index (AET, actual evapotranspiration) and island area, i.e. Wright estimated the gross amount of energy provided by islands of greatly varying area. As numerous other variables are known to vary with area across such a range of island sizes, the analysis is, for present purposes (detection of peaks in richness at intermediate levels of productivity) confounded. Thus, while Mittelbach et al. (2001) report that they could detect no evidence of plot-size or plot-size extent interactions on the form of the plant SRPR (species richness–productivity relationship), their analysis would make a more useful contribution to diversity theory if organized by grain rather than extent. Indeed, it is difficult to know what interpretations can be drawn from data so organized (cf. Dungan et al. 2002).

#### *Surrogate measures of productivity*

Direct measurements of net primary productivity (NPP) are hard to attain, especially at coarser scales. Hence, the meta-analysis of necessity relied on sur-

rogate variables, including biomass, rainfall, AET (actual evapotranspiration), nutrients, and ‘other.’ Unfortunately, these variables were treated as directly substitutable for productivity. The assumptions involved in doing so are problematic. For instance, while a positive relationship may hold between rainfall and productivity for a particular data set across a given range of rainfall values, this linear “model” is clearly incomplete (see Scurlock and Olson 2002). Indeed, there is evidence in the literature from which the meta-analysis has been compiled, that systematic variations in energy regime in relation to rainfall can mean that unimodal relationships between rainfall and richness are consistent with—and even supportive of—an underlying positive, monotonic relationship between productivity and richness (e.g., Kay et al. 1997; also see *Case studies . . .*, below). Biomass is also an ambiguous indicator of productivity, as forest stands can have the same biomass with very different levels of stand turnover (cf. Phillips et al. 1994, Whittaker et al. 1999). Of the surrogates used, only AET would seem to be a fairly straightforward surrogate for productivity (references in O’Brien [1993]).

#### *Statistical issues*

Mittelbach et al. (2001) use both ordinary least squares (OLS) regression and generalized linear model (GLM) regression (with the Poisson distribution and a logarithmic link function), preferring the latter for the bulk of their analyses. Model selection was undertaken by reference to a *t* ratio statistic, and the maximum complexity tested for was the quadratic term, i.e. they tested for positive, negative, or unimodal (humped, or alternatively U-shaped) forms. We agree that GLM is preferable for this task, but raise two concerns. First, Mittelbach et al. (2001, p. 2384) use a significance level of 10% ( $P < 0.1$ ) to “. . . be as liberal as possible in discovering patterns . . .” Typically, studies of species-richness patterns use a critical value corresponding to  $P = 0.05$  or 0.01. We examined Mittelbach et al.’s results (their Appendix A), and found that the ratio of quadratic terms to linear and intercept terms are strongly reduced with decreasing significance level, i.e., 1.26, 0.89, and 0.67 for the  $P$  values 0.1, 0.05, and 0.01, respectively. This shows that the *patterns detected in the meta-analysis are dependent on the significance level chosen*. Although the choice of  $P = 0.1$  is by no means incorrect in itself, it will make the meta-analysis biased towards more complex relationships. Second, and of greater concern, is their neglect of the scale parameter ( $\phi$ ) in using the Poisson GLM. With the Poisson distribution we assume that the variance equals the mean ( $\phi = 1$ ). However, in biology the variance is frequently greater than the mean, i.e., overdispersion occurs ( $\phi > 1$ ) (Legendre and Fortin 1989). This phe-

nomenon results in statistical bias when used in a classic  $\chi^2$  test of deviance (see McCullagh and Nelder 1989). Similarly, overdispersion affects  $t$  tests, as used by Mittelbach et al. (2001). To illustrate this we analyzed by Poisson regression 1000 randomly simulated relationships with 100 observations each, i.e.,  $y_{ij}$  and  $x_{ij}$  where  $i = 1 \dots 100$ , and  $j = 1 \dots 1000$ . The response variables ( $y_j$ ) were Poisson distributed with  $\mu = 50$ , and a new but overdispersed data set was generated by  $z_{ji} = [1.5(y_{ji} - 50)] + 50$ . The response variables  $y_j$  and  $z_j$  have a similar mean but different variance, the scale parameters being  $\phi = 1$  and 2.3, respectively. The Poisson data ( $y_j$ ) generated 14, 46, and 99 significant relationships for  $P = 0.01, 0.5$ , and 0.1, respectively, whereas the overdispersed data ( $z_j$ ) gave 52, 143, and 195 significant relationships, respectively. The expected number of relationships detected by chance is 10, 50, and 100 respectively, i.e., the  $t$  tests on overdispersed data ( $\phi \approx 2.3$ ) are much too liberal. Adjustment for overdispersion is done by standardization of the change in deviance by the scale parameter,  $(D_0 - D_1)(\phi(n - p))^{-1} \sim F_{\alpha, p - q, n - p}$  (where  $p$  is the number of parameters in the model) (Venables and Ripley 1997, Myers et al. 2002). By comparison, the scale parameters for the Currie and Paquin (1987) and O'Brien (1993) data sets (re analyzed below) were 16 and 49, respectively. Therefore, the number of unimodal relationships detected by Mittelbach et al. (2001) may be artificially increased for this methodological reason, quite apart from the other issues raised herein, but we are unable to evaluate the magnitude of this problem from the information given.

*Case studies from the meta-analysis: Tree data at regional to global scales*

We next examine those studies from the meta-analysis that were deemed to be: (1) tree data (in some cases "trees and shrubs"); (2) regional or continental-global in scale; and (3) evidence of unimodal or negative SRPR (species richness-productivity relationship). There were eight such studies (seven humped, one U-shaped, none negative) as against only four classed as demonstrating a positive relationship, and two for which no consensus was reached (Mittelbach et al. 2001: Appendix A [*Consensus summary*]).

*Case 1.*—Currie and Paquin's (1987) analysis of North American tree species richness is a macro-scale study, using cells of  $\sim 50\,625$  km<sup>2</sup> to 96 000 km<sup>2</sup> (J. Kerr, *personal communication*). Currie and Paquin, using a nonlinear (logistic) regression, demonstrate a positive relationship of richness with increasing AET (actual evapotranspiration; the surrogate index of productivity). Mittelbach et al., using GLM and the Poisson distribution, classify these data as supporting a hump-shaped pattern due to a negative quadratic term. We

reexamined the original data, kindly provided by David Currie upon our request, and a scanned data set taken from Currie and Paquin (1987: Fig. 2), as this was the approach to data capture used by Mittelbach et al. Of 336 data points, just 275 and 268 were recovered by us and by Mittelbach et al., respectively. By forward selection (the Poisson regression) a negative quadratic term gave the best fit for both the original data (residual df = 333,  $F = 19.9$ ,  $P < 0.001$  ( $P_{\text{cubic term}}$  [i.e.,  $P$  when including a cubic term as well as the quadratic term] = 0.381), AIC (Akaike Information Criterion) = 4848 ( $\text{AIC}_{\text{cubic term}} = 4867$ ),  $\phi = 15.76$ ), and our scanned data (residual df = 272,  $F = 5.2$ ,  $P = 0.024$  ( $P_{\text{cubic term}} = 0.207$ ), AIC = 4000 ( $\text{AIC}_{\text{cubic term}} = 4005$ ),  $\phi = 14.68$ ). Both the  $F$  test and the AIC were adjusted by the scale parameter (Venables and Ripley 1997). Although a negative quadratic term was included, no peak in richness for either data set was detected within the measured range of AET (Fig. 1a). Allowing more terms to be included, a 5<sup>th</sup>-order polynomial was found by both AIC and  $F$  test for the original data, suggesting a peak, but with great uncertainty at high AET indicated by the bootstrap 95% confidential interval (Fig. 1b, Efron and Tibshirani 1993). A test for outliers suggests that three observations ("x" in Fig. 1a) can be considered outliers: when they were removed, a positive trend in richness with AET appeared (Fig. 1b), and from the bootstrap-sampled data sets the probability of a peak occurring within the observed range is very small ( $P = 0.0771$ ). A similar conclusion was found for the scanned data, but here the indication of a mode was more pronounced (Fig. 1c), suggesting that error in classifications may result from the loss of data in scanning over-plotted data. It may be debated whether the outliers are indicative of a missing variable, are a failing of AET as a simple productivity surrogate, or are genuinely part of the signal in the data set. In any case, we note that by the model complexity (unimodal, i.e., quadratic term) allowed by Mittelbach et al. (2001), a peak in richness within the observed range of AET is not supported in these data (original or scanned). Therefore, we find no reason to reject the original interpretation by Currie and Paquin (1987) of a positive SRPR.

*Case 2.*—A globally distributed data set from Latham and Ricklefs (1993) also uses AET for productivity, and is classed as a hump-shaped SRPR. However, Latham and Ricklefs (1993) show that the decline in richness, which occurs only above 900-mm AET, is due entirely to a few samples of comparatively small sample area, all from eastern North America. In this data set, region (of the globe) and the substantial variation in sample area, from 17 km<sup>2</sup> to 7401 km<sup>2</sup> (two orders of magnitude), combine to invalidate the use of the data in the meta-analysis.

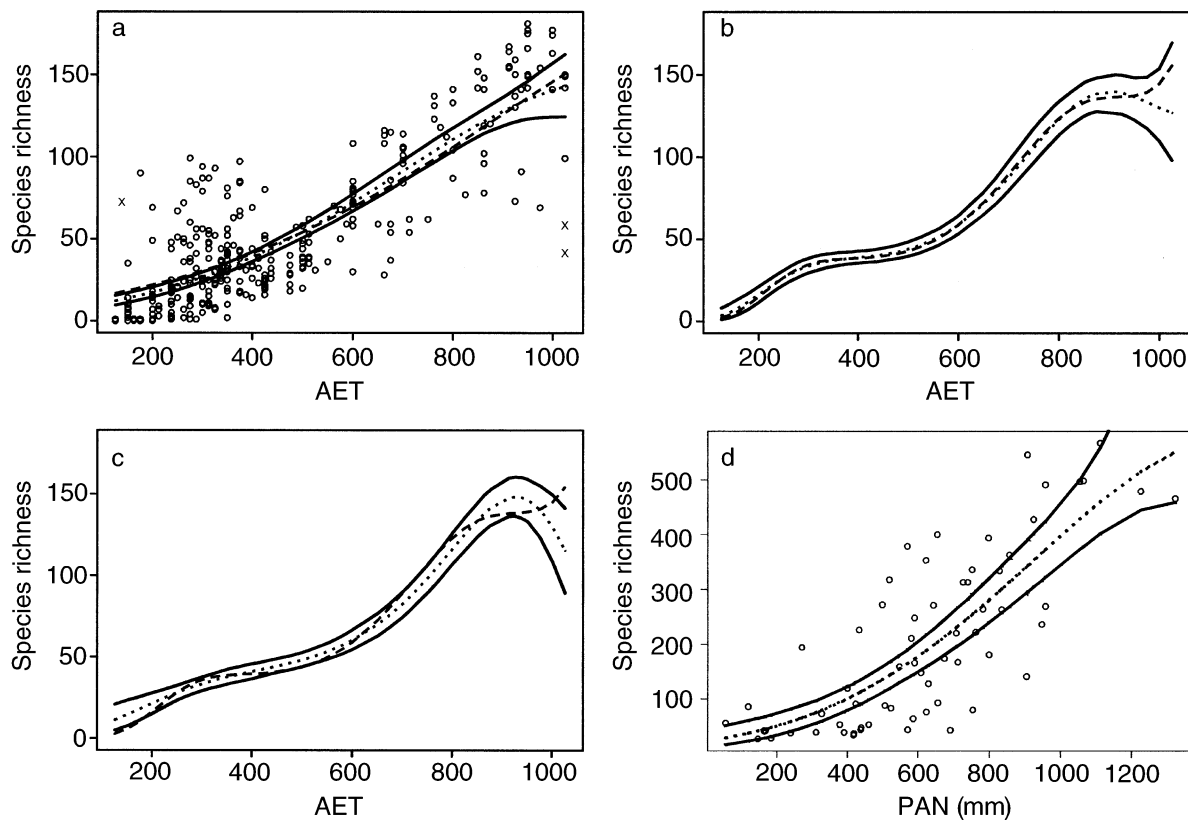


FIG. 1. Results of reanalysis of two case studies from the Mittelbach et al. (2001) meta-analysis of studies examining the relationship of species richness to productivity. (a) Currie and Paquin (1987): the quadratic-term richness–AET (actual evapotranspiration) relationships; original data (dotted line) with 95% confidence intervals (CI; solid lines), and data scanned (dashed line) from their Fig. 2. (b) Currie and Paquin (1987) original data: 5th-order polynomial (dotted line) of richness and AET, showing the great uncertainty indicated by the bootstrap 95% pointwise CI (solid lines). Deletion of the outliers (“x” in Fig. 1a) removes the peak (dashed line). (c) Currie and Paquin (1987) scanned data: A peak is evident by a 4th-order polynomial (dotted line) (solid line = 95% pointwise CI). Deletion of potential outliers removes the peak (dashed line). (d) O’Brien (1993): No peak in woody-plant species richness was detected in relation to the given range of PAN (annual rainfall);  $E(\text{richness}) = \exp(3.14 + 0.0423[\text{PAN}] - 0.00000138[\text{PAN}]^2)$ .

*Case 3.*—A southern African “tree” data set of 65 equal-area grid cells of about 25 000 km<sup>2</sup> (O’Brien 1993, O’Brien et al. 1998) is unequivocally macro- or regional scale. Mittelbach et al. (2001) take annual rainfall (PAN) as the surrogate for productivity and, setting aside the reported positive linear relationship between rainfall and richness (O’Brien 1993), classify this study using GLM as a unimodal SRPR. We dispute this on three grounds. First, our statistical reanalysis shows no basis for classifying this relationship as unimodal. The negative quadratic term was barely significant (residual df = 62,  $F = 4.5$ ,  $P = 0.039$  ( $P_{\text{cubic term}} = 0.383$ ),  $\text{AIC} = 3285$  ( $\text{AIC}_{\text{cubic term}} = 3344$ ),  $\phi = 48.98$ ), and minute in comparison with the linear term, i.e., only adjusting the positive trend (Fig. 1d). Second, the probability of a peak occurring within the observed range of PAN is low:  $P(\text{peak within range}) = 0.1530$

by 10 000 bootstrap samples. Third, in any case, PAN is an imperfect surrogate for NPP across this study area. Plant activity depends on both rainfall and energy regime and there is sufficient variation in both across the study region for this to matter—indeed O’Brien’s (1993, 1998) analyses demonstrate the necessity of capturing the dynamic interplay of rainfall and energy in modeling richness globally. Her analyses demonstrate that the two-variable PAN+PEMIN-PEMIN<sup>2</sup> model (where PEMIN = Thornthwaite’s minimum monthly potential evapotranspiration) is a significantly better descriptive model for richness than any other one- or two-variable model considered—including models based on AET. A unimodal SRPR is not inherent in O’Brien’s (1993) data; instead, her analyses provide evidence entirely consistent with the existence of a positive, monotonic SRPR.

*Case 4.*—The study by Hughes et al. (1996) is based on the distribution pattern of the midpoints of species ranges, analyzed in relation to modeled rainfall data. This is an indirect, almost aspatial approach to a spatial problem, making it hard to evaluate in this context. The study is restricted to *Eucalyptus* (819 species), a genus characteristic of dry-land or sub-tropical moist ecosystems, but unrepresentative of the diverse wet tropical rain-forest ecosystems of the eastern seaboard, i.e., not capturing the full response of trees to the Australian climate envelope (cf. Specht and Specht 1989).

*Case 5.*—Cao and Peters (1997) provide data on diversity of Chinese beech forests using local-scale plots (300 m<sup>2</sup> to 2300 m<sup>2</sup>) from 10 forests; in two forests a separate sampling was undertaken at contrasting altitudes. Both the number (1 to 5) and the size of plots varied, making it impossible to control for sampling variation in evaluating the data presented. Cao and Peters (1997) report that energy regime, and in particular cold-related disturbances, were strongly related to diversity of the sites (assessed using diversity indices, not richness). Thus, the inclusion of this study in the meta-analysis, and the use of PAN as the productivity surrogate, appears to be unwarranted.

*Case 6.*—Kay et al. (1997), in their analyses of South American forests, used 37 of 69 “Gentry” 0.1-ha plots originally reported by Clinebell et al. (1995)—definitely for trees a local grain study. The original analyses suggest a strong positive relation with PAN up to ~4000 mm, and thereafter a plateau in richness. There were only four observations for >4000-mm PAN. Mittelbach et al.’s GLM analysis returned a unimodal SRPR. When productivity is represented by surrogate variables there is a danger of circular reasoning in debating richness–productivity–climate relationships. However, Kay et al. (1997) usefully provide data for a direct index of productivity: leaf litter fall. This separate tropical data set demonstrates increased productivity with higher rainfall up to ~2500 mm PAN, and thereafter, a gradual decline with increasing rainfall (albeit with high variance). The decline was suggested to be due to less energy (high cloud cover) and/or nutrient availability (high leaching). Thus, depending on the range of values considered, a unimodal relationship between richness and rainfall is not evidence of a unimodal relationship between richness and productivity—indeed we should anticipate a plateau (and/or decline) in richness and productivity at high rainfall levels, as beyond a certain point water ceases to be limiting and variation in energy regime becomes critical (cf. Scurlock and Olson 2002). Further, the tree richness in the 0.1-ha-plot data declines sharply with altitude, corresponding with the transition from lowland to montane forests, again reflecting changes in the energy regime. The failure to account for interactions between water

and energy (O’Brien 1993, 1998) in the meta-analysis is a likely reason for the increased proportion of unimodal relationships detected by Mittelbach et al. (2001: 2391: column 2) with increased range of annual rainfall. The circumspection necessary in using PAN as a global productivity surrogate is evident from Esser (1998).

*Case 7.*—The analyses by Phillips et al. (1994) are again local scale in grain, using variable area plots “corrected” to species per hectare (the pitfalls in such corrections are shown by He et al. [2002]). Their combined tropical South America, Asia, and Africa data set was again classed as a humped SRPR based on PAN data, values for which ranged up to 4000 mm, invalidating the use of PAN as a simple surrogate for productivity (see case 6, above).

*Case 8.*—A regression model given by Williams et al. (1996) for woody species richness, based on 400-m<sup>2</sup> (i.e., local-scale) data from Australia, was wrongly classified in the meta-analysis as a U-shaped SRPR, when it should have been a positive relationship. The model is woody-plant richness =  $-0.718 + 0.0060[\text{PAN}] + 0.000005[\text{PAN}]^2 - 0.00217[\text{clay}]^2$  [topsoil clay content],  $r^2 = 0.30$ . The classification of this study as U shaped contradicts the protocol of the meta-analysis, which requires an internal minimum in richness in relation to PAN (Mittelbach et al. 2001: 2384); in this instance the minimum richness of minus two species does not occur until PAN drops to minus 600 mm, an empirical impossibility on two counts. As an aside, Williams et al. (1996) report a unimodal relationship between deciduous-tree species richness and rainfall within this local-scale data set, which reflects the decline in this life form as evergreen trees become predominant in the wet tropical forests of Australia.

There were six more regional/global tree-data sets in the meta-analysis. For two, no overall pattern could be discerned. Four were classed as positive SRPR. Of the latter, the first data set was taken from the same paper as case 7 (above), and thus has the same limitations: it consists of 13 plots from South America, varying from 0.6 to 12.4 ha in area. The remaining data sets derive from Adams and Woodward (1989) and are based on quadrats of 66 000 to 81 000 km<sup>2</sup> (mean of 72 000 km<sup>2</sup>). Primary-productivity values were calculated using the Chickugo model, using global net solar-radiation maps and annual precipitation. The three study areas analyzed were Europe, North America, and East Asia. Clear positive SRPR were reported in each case.

In summary, we have reexamined the eight studies from the meta-analysis that were (1) for “trees,” (2) regional or continental to global in “scale,” and (3) unimodal in SRPR. We contend that none of these studies should be so classified. Only cases 1 and 3 are regional in scale, in the sense of the grain or focus of

the study. Case 4 uses an unrepresentative taxonomic group. Cases 3–8 involve the use of PAN as a simple surrogate for productivity, which is both theoretically and empirically unsound. Case 8 has been misreported and doubts attend the classification of others (e.g., cases 1, 2, 3, 5) due to inadmissible sampling designs and/or analytical problems. By contrast, of the four positive SRPRs discussed, three of them appear to fit the criteria of being (1) for trees, (2) macro-scale, (3) having scale held approximately constant, and (4) using an adequate productivity surrogate.

### Conclusions

Meta-analyses are difficult: this one—Mittelbach et al. 2001—has the virtues of clarity of objectives and transparent presentation. However, it does appear that significant problems attend the treatment of scale, and the selection, capture, and analysis of data sets. More powerful models or crucial additional variables (e.g., see O'Brien 1993, Williams et al. 1996, Kay et al. 1997, Scurlock and Olson 2002) necessary for the interpretation of the species richness–productivity relationship (SRPR) have been overlooked. For trees, at the macro-scale, we believe that rather than constituting the dominant empirical pattern (7 out of 12 studies), there is in fact no evidence in support of a hump-shaped relationship. Several of our criticisms are restricted to this small subset of the much more extensive meta-analyses by Mittelbach et al. (2001). However, as the remainder of their meta-analysis involves the same data-capture techniques, the same analytical tools (which are too liberal towards unimodal patterns), and the same oversimplified approach to the use of surrogate variables, we call for caution in citing their findings and for a reexamination of other sections of the meta-analysis. In doing so, we stress that we anticipate that their general findings will stand: the form of the SRPR varies as a function of scale (Chase and Leibold 2002) and taxon.

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## WHAT IS THE OBSERVED RELATIONSHIP BETWEEN SPECIES RICHNESS AND PRODUCTIVITY? REPLY

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We appreciate the opportunity to reply to Whittaker and Heegaard's (2003) comment. Whittaker and Heegaard (hereafter W&H) bring up a number of important points regarding the analysis of species richness–productivity relationships (SRPRs). Some of their comments apply in broad fashion to any analysis of SRPRs, whereas others are directed specifically at our published review (Mittelbach et al. 2001). The relationship between productivity and species richness remains perhaps the most controversial of the diversity patterns (Rosenzweig 1995) and W&H have done much to help elucidate this relationship in their own research. We

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agree with many of W&H's general comments, particularly that there is no single, universal SRPR and that patterns are scale dependent, and we acknowledge their efforts to improve our understanding of SRPRs. However, we disagree with W&H on a number of specific issues and we discuss these in our reply below.

It is important to preface our reply by reiterating, as W&H note, that our study was the first attempt at a broadly inclusive literature review and meta-analysis of SRPRs. Previous reviews of the SRPR were usually based on selected examples, often used to support a particular point of view (e.g., the hump-shaped SRPR). In our analysis, we therefore broadly scoured the literature and applied standardized criteria to characterize the form of each SRPR. However, as we note in our paper (and as W&H point out as well), the literature on SRPRs is heterogeneous and far from ideal. Any attempt at a meta-analysis of SRPRs will involve decisions on how to treat the data and invariably compromise. W&H take issue with some of our analytical methods, which they feel were too liberal towards detecting unimodal (hump-shaped) patterns. We examine this issue below and then discuss their more general concerns about the impact of scale and surrogate measures of productivity on SRPRs. Because W&H's comments focus on plants (trees in particular), we will limit our response to these groups as well, although our original review included both animal and plant studies.

### *Statistical issues*

In our review we used a significance level of  $P \leq 0.10$ , rather than the more typical  $P \leq 0.05$ , to classify SRPRs as either positive, negative, unimodal (humped), U-shaped, or not significant (using both OLS [ordinary least square] and GLM [general linear model] regressions). We chose the more generous  $P$  value because

we wanted to be as liberal as possible in discovering patterns. W&H suggest that this choice of significance level biases our meta-analysis toward finding complex relationships, and they offer as support their calculations showing that SRPRs with lower  $P$  values tended to have smaller quadratic terms relative to their linear and intercept terms (SRPRs taken from Mittelbach et al. [2001]). W&H's concern over our choice of  $P$  values is certainly reasonable. Therefore, we re-plotted our original figure for SRPRs in vascular plants at all spatial scales (extents) using both  $P \leq 0.05$  or  $P \leq 0.10$  significance levels (Fig. 1). While there are some small differences, the overall patterns are very similar.

W&H note that our use of a GLM with an assumption of Poisson errors and a logarithmic link function does not account for possible overdispersion of the data (i.e., variance higher than the mean). They go on to show that such overdispersion may make the detection of significant SRPRs more likely. We did not examine the amount of overdispersion in the data reported in each of the original studies (in many cases this would not be possible) and we acknowledge this limitation to our analysis. However, it is not clear what effect this has on our general conclusions. W&H suggest that the number of unimodal relationships we report may be artificially increased because of this problem. However, failing to account for overdispersion in the data when it exists will lead to finding more significant SRPRs of all forms: positive, negative, or modal. Thus, while W&H's criticism is valid, it does not imply that our analysis is biased towards detecting any particular form of the SRPR.

*Case studies from the meta-analysis:  
Tree data at regional–global scales*

W&H question the evidence for any relationship other than a monotonically positive one between tree species richness and productivity at broad (regional to continental) spatial scales. They provide a detailed re-analysis and critique of each of the eight broad-scale tree studies that we classified as hump-shaped ( $n = 7$ ) or U-shaped ( $n = 1$ ) in our original review (Mittelbach et al. 2001). They give a shorter critique of the four relationships that we classified as positive SRPR. They go on to eliminate all but three studies based on a variety of criteria including: varying plot sizes within a study, inappropriate (too small) plot sizes (e.g., Gentry's 0.1-ha forest plots [Phillips and Miller 2002]), and inappropriate measures of productivity. Of the remaining studies that satisfy W&H criteria for what is appropriate, three SRPRs are classified as positive (all from Adams and Woodward's (1989) study on tree species richness in temperate areas of Europe, North America, and East Asia. The other two studies, Currie and Paquin (1987) for North American trees and

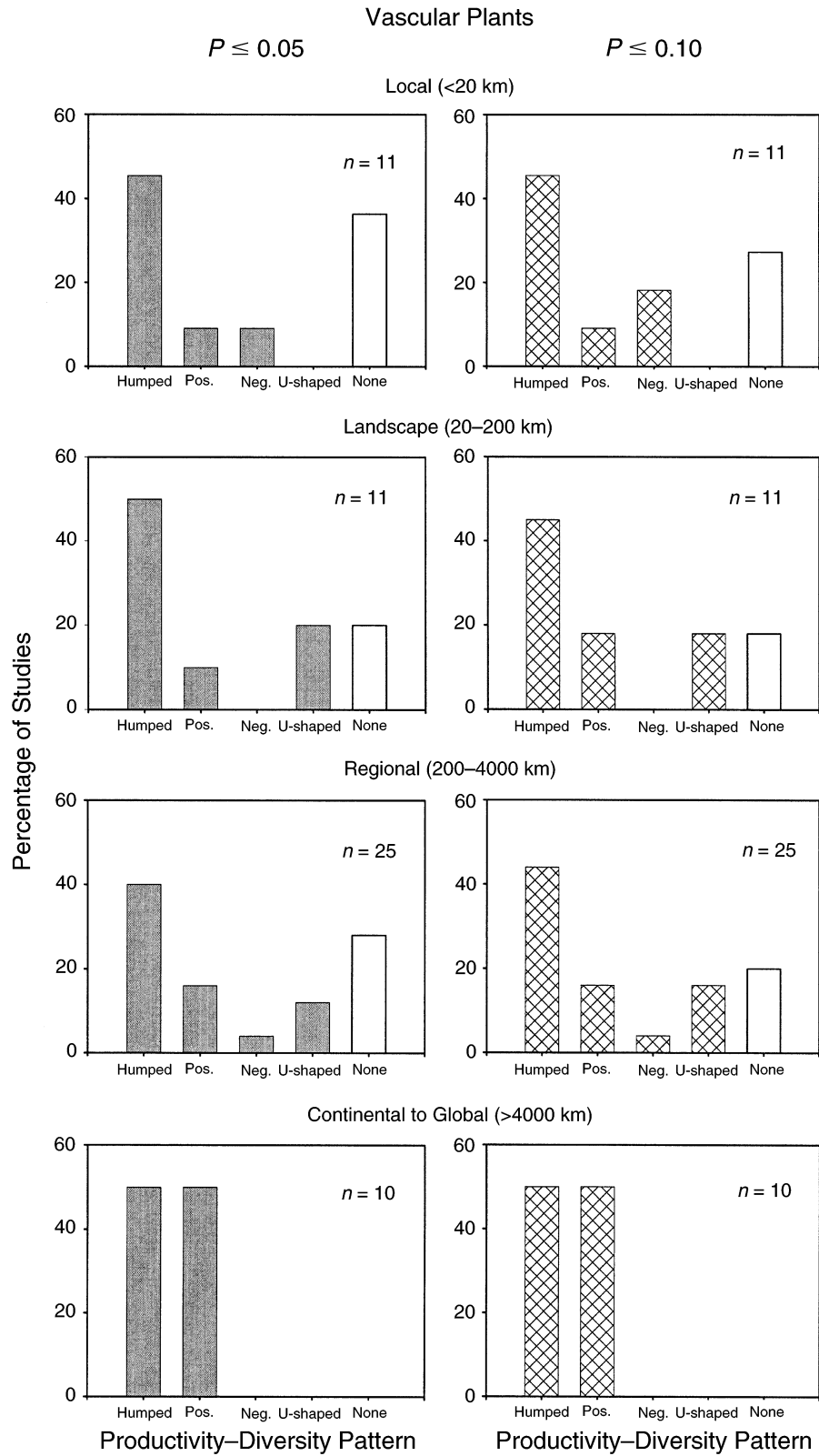
O'Brien (1993) for woody plants in southern Africa, have SRPRs best fit by a regression containing a significant, negative quadratic term (i.e., a decelerating trend). W&H argue, however, that the impact of the quadratic term is minor in these studies and that there is no evidence of a peak (hump) occurring within the observed productivity range. Our original analysis of these patterns concluded that these curves contained an internal peak [based on the MOS-test; Mitchell-Olds and Shaw (1987)].

We agree with W&H that surrogate productivity measures and varying plot sizes can confound interpretations of SRPRs. However, W&H's reanalysis of the broad-scale "tree" SRPRs seems too much like special pleading in support of a particular point of view. Intense scrutiny of individual studies and the elimination of "inappropriate" examples can increase rigor, but the selection criteria must be set out at the beginning of the meta-analyses and must be applied equally to all studies. Instead, W&H were critical of only those studies that fail to support a positive trend. We disagree with a number of their specific criticisms.

For example, eliminating "outliers" from a data set should only be done if there is reason to believe these points represent errors of measurement—otherwise, the points are part of the data (W&H's cases 1 and 2). In a separate issue, W&H suggest that all studies in which plot size varied significantly are invalid, because variation in plot size within a study can bias the analysis of diversity relationships. However, unless such variation is systematic it should lead to the failure to find a pattern, not to preferentially finding a hump-shaped pattern (W&H's case 5). Finally, W&H suggest that the study of Hughes et al. (1996; W&H case 4) should be eliminated because restricting the analysis to the genus of *Eucalyptus* (consisting of 819 species) somehow makes these data "unrepresentative." However, many data sets are based on only a portion of the plant (or animal) community and the argument could be made that considering only "tree" data sets fails to examine the response of the whole plant community to a productivity gradient (see Waide et al. [1999] for discussion of this point). At least one theory (the inter-taxonomic competition hypothesis; Rosenzweig and Abramsky 1993), explicitly predicts that within a single clade the productivity–diversity relationship will be hump-shaped. However, we agree that the study of Hughes et al. (1996) is somewhat ambiguous with regard to how *Eucalyptus* richness and rainfall are spatially associated and that the SRPR derived from this study is open to question.

One can argue with the criteria we employed in selecting studies for our analysis. On the other hand, it is important not to miss the forest for the trees. The main point of our paper was to test the general claim





that hump-shaped SRPRs are ubiquitous at all scales and in all systems. This is clearly not true. Both unimodal and positive relations are common. We do not pretend to have the final word on what the patterns are. Our data set, as extensive as it is, is still quite limited and we expect, for example, that the percentage of studies showing particular relationships (e.g., Fig. 1) will change using different criteria for analysis and as more data become available. We welcome additional analyses and expect differing interpretations.

W&H's analysis of "tree" patterns does raise the very interesting question of whether the magnitude of hump-shaped relationships varies systematically with taxonomic group or spatial scale. For example, are there differences in the magnitude of the observed quadratic terms for SRPRs in grasslands compared to forests, or at local vs. continental scales? The strength of the quadratic terms is a legitimate issue separate from its existence and this is not something we attempted to address in our meta-analysis. It may be that tree diversity at broad spatial scales shows relatively little (or no) decline in species richness with productivity compared to other taxa or compared to other spatial scales. We agree with W&H that most of the current data for woody-plant species richness across broad spatial scales shows a general, positive trend with productivity. However, a number of the observed relationships exhibit high variability at increased productivity, and (at least by our stated criteria) some are peaked.

#### *Scale*

W&H suggest that grain is the only scale variable by which one should examine productivity–diversity relationships. However, a comprehensive understanding of SRPRs will require examining all three components of scale—grain, extent, and focus. In a study of SRPRs for plants in Wisconsin, Scheiner and Jones (2002) were able to independently manipulate the three components of scale and found that their effects on SRPR differed. In Mittelbach et al. (2001) we confined our analysis to extent because that scale component was most accessible from the literature, was pertinent to many of the theories concerning SRPRs, and was directly relevant to one purported cause of the failure to find hump-shaped patterns, the pattern accumulation hypothesis (Scheiner et al. 2000).

W&H are correct in cautioning that studies measuring species richness in small plots potentially examine

very different mechanisms than do studies measuring species richness over large spatial scales. As Huston (1999) notes, species interactions are likely to play a strong role in determining richness in small plots, whereas other mechanisms (including speciation and extinction) may affect species richness measured on the scale of thousands of square kilometers (see also Whittaker et al. 2001). There is a tendency for grain and extent to be correlated across studies of SRPRs. Wright et al. (1993) mentioned this in their review and we specifically noted this correlation in our original study (Mittelbach et al. 2001). If we look at the 100 data sets from Mittelbach et al. (2001) that contain information for both scale parameters, we find that the correlation between grain and extent is positive, but weak ( $r = 0.25$ ). In Mittelbach et al. (2001), we used logistic regression to test whether the probability of detecting a particular form of the SRPR (e.g., positive or hump shaped) depended on plot size, spatial extent, or their interaction. We found that it did not. Hawkins et al. (2003a) recently examined the influence of grain size in determining the ability of climatic variables to explain species richness patterns for plants and animals at broad spatial extents (>800 km of linear distance). They considered studies using two sampling resolutions (grain sizes)—species richness estimated from sampled plots (small grain) and species richness determined from range maps (large grain). Somewhat surprisingly, they found that the average amount of variance in species richness explained by climatic variables was the same in both cases ( $r^2 = 63.3 \pm 2.4$  for range maps vs.  $r^2 = 63.6 \pm 3.4$  for sampled plots [mean  $\pm 1$  SE]). There are no easy answers to the question of how to combine studies that use different sampling methods in any meta-analysis of SRPRs. W&H's cautions are duly noted. However, we can find no evidence that our general conclusions about SRPR at different spatial extents are the result of inappropriately combining studies of different grain size.

#### *Surrogate measures of productivity*

Estimates of productivity at large spatial scales usually rely on surrogate variables correlated with productivity. W&H are especially critical of the use of annual precipitation (PAN) as an index of productivity. We agree with W&H that productivity (net primary productivity, NPP) and PAN are not linearly related over the entire range of PAN. Fitted relationships be-

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FIG. 1. Percentage of published studies on vascular plants showing various patterns of species richness and productivity at four geographical scales (data from Mittelbach et al. 2001). The right-hand column shows relationships classified as significant at  $P \leq 0.10$ , and the left-hand column shows relationships classified as significant at  $P \leq 0.05$ . Samples sizes ( $n$ ) refer to the total number of relationships analyzed in each case.

tween NPP and PAN tend to be linear up to about 1500 mm PAN and to plateau above 3000 mm (Scurlock and Olson 2002). In areas of very high precipitation, NPP may be limited by temperature, light, or other factors. However, a linear relationship between PAN and productivity is not necessary for our analysis, we only assume that the relationship is monotonic over the range of the data set. Therefore, it is wrong to dismiss a study simply because it used PAN as a surrogate of productivity. However, W&H are correct in questioning studies where the form of the SRPR may be driven by a few, very high values of PAN (e.g., our classification of Kay et al. 1997). W&H's comment that "Biomass is also an ambiguous indicator of productivity, as forest stands can have the same biomass with very different levels of stand turnover. . .", is also true. However, in our review, the vast majority of the studies using biomass as a measure of productivity were conducted in herb-dominated plant communities within an ecoregion (e.g., temperate grasslands). In these systems, peak standing-stock biomass is correlated with annual NPP (Scurlock et al. 2002).

A better understanding of the relationship between species richness and productivity, particularly at large spatial scales, will depend on more refined measures of productivity. Recent work by Francis and Currie (2003) and Hawkins et al. (2003a, b), as well as earlier studies by O'Brien (1993), show that broad-scale patterns of terrestrial plant richness are best correlated with climatic variables related to water-energy dynamics (e.g., both temperature and water availability). However, many of these predictive relationships are nonlinear. Studies of species richness patterns are enjoying renewed interest (e.g., Allen et al. 2002, Francis and Currie 2003, Hawkins et al. 2003a, b, Hurlbert and Haskell 2003, Willig et al. 2003), driven in part by new tools (e.g., GIS mapping, satellite imagery, and remotely sensed measures of productivity [NDVI] and other environmental variables) that combine to make the analysis of broad-scale patterns in species richness and productivity easier and more exact. The next few years should see a significant increase in the number of available data sets compared to what we had to work with in our review.

### Conclusions

W&H suggest that our analysis of SRPRs is too liberal towards detecting unimodal relationships. However, while we agree that there are areas where our analysis could be improved, we see no evidence of bias towards finding one type of SRPR over another. W&H also argue that we should have been more restrictive in choosing studies for our meta-analysis; for example, excluding all studies with variable plot sizes or studies that used an "imperfect" surrogate of productivity. We

agree that many of the studies in our review have failings and that they could be rejected for one reason or another. However, the flip side of such a stringent approach is that it severely limits the data base. For example, if we look at SRPRs for terrestrial plants and eliminate all studies that contain variable plot sizes and all studies that use annual rainfall >1500 mm as a surrogate of productivity, we are left with 28 studies conducted at spatial extents <4000 km (our local-regional scales). For these 28 SRPRs, 39% are hump shaped, 21% are positive, 4% are negative, 4% are U-shaped, and 32% are not significant ( $P > 0.05$ ). Gratifyingly, the pattern in these restricted data is consistent with the general findings reported in Mittelbach et al. (2001); at geographical scales smaller than continents, hump-shaped relationships predominate and positive relationships are the next-most-common SRPR.

W&H contend that there is no evidence that woody-plant richness declines with increased productivity at large spatial scales. However, W&H's criteria basically whittle the continental-global data set down to two studies that correlated tree species richness with estimated productivity: Currie and Paquin (1987) and Adams and Woodward (1989). These studies report four SRPRs, two of which are based on the same North American tree data. The SRPRs are all positive and (to varying degrees) nonlinear. Should we conclude from this limited data set that woody-plant diversity never declines with productivity over broad spatial scales? Possibly. However, we believe that the jury is still out on this one. We agree that in most cases, the evidence for humped-shaped SRPRs for trees at broad spatial scales is based on relatively few data points at the highest productivities. This is a limitation of the studies available. Future analyses based on additional studies using better estimates of productivity and conducted over broader climatic gradients (temperate zone to tropics) may show that tree species richness only increases with productivity at continental-to-global scales. However, at this point we stand by the general conclusions of Mittelbach et al. (2001), namely, that hump-shaped relationships predominate for plants at small spatial extents, that positive productivity-diversity relationships became relatively more common at large spatial extents, and that both positive and hump-shaped relationships occur at large scales.

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