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Fewer species because of uncommon habitat? Testing the species pool hypothesis for low plant species richness in highly productive habitats

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Numerous studies have reported a significant pattern of decreasing plant species richness across regional habitat gradients of increasing productivity or community biomass (Grace 1999, Waide et al. 1999). The interpretation of this pattern has been the focus of several hypotheses (see reviews by Rosenzweig and Abramsky 1993, Abrams 1995, Grace 1999, Aarssen 2001) but none that have emerged with strong supporting evidence. In this article we propose a simple method for evaluating one of these hypotheses and illustrate its application using published data.

The 'species pool' hypothesis was proposed by Taylor et al. (1990) in response to the 'competitive exclusion' hypothesis of Grime's (1973, 1979) 'hump-backed' model. Grime's model postulates that the commonly reported decline in plant species richness with increasing habitat productivity is explained by an increasing intensity of competition for resources, causing increasing competitive exclusion. The species pool hypothesis, however, explains this variation in plant species richness in terms of variation in the historical opportunity for origination of adapted species, i.e. species that can complete their life cycle and recruit offspring under the prevailing selection pressures, including competition, associated with a given habitat type. Because speciation requires space and time, we may expect that relatively few species have evolved with adaptation to the selection pressures of habitat types that have been uncommon over evolutionary time, i.e. habitat types that are relatively rare (in terms of spatial extent) or relatively young (with a short geological history). Such habitat types may be expected, therefore, to have relatively few contemporary resident species (see also Ricklefs and Schluter 1993). Accordingly, the species pool hypothesis predicts that resident plant species richness in highly productive habitats is relatively low because these habitat types are relatively young in geological age and/or small in terms of historical land area on a global scale (Taylor et al. 1990, Aarssen 2001).

The central question from this hypothesis remains unanswered: Are habitat types with relatively high productivity not only relatively low in species richness but also relatively uncommon? The principal determinant of variation in potential vegetation productivity between habitats is the resource-supplying power (e.g. substrate fertility) of the habitat (Taylor et al. 1990). The species pool hypothesis predicts that the frequency distribution of historical land area of different habitat fertility or productivity types should approximate some kind of unimodal central tendency; i.e., with the most common habitat productivity type over evolutionary time being of some intermediate level and with the most extreme (both low and high) productivity types being the least common. Given that this distribution has no definable upper limit and is strictly bounded only at the left end (i.e. habitats cannot have less than zero productivity), the predicted frequency distribution of habitat productivity types should be right-skewed unimodal, analogous to the 'left wall' effect proposed for the evolution of organismal complexity (Gould 1988). On this premise, the species pool hypothesis would predict that past opportunity for origination of adapted species and hence, contemporary resident species richness should also be generally highest in habitats with somewhat less than intermediate productivity (compared with extremely low or high productivity) (Taylor et al. 1990; see also Rosenzweig and Abramsky 1993, Abrams 1995, VanderMeulen et al. 2001). The latter is indeed the case for contemporary plant species richness patterns recorded in numerous studies reporting a unimodal or right-skewed unimodal 'hump-shaped' relationship (Grace 1999).

Below, we develop a quantitative approach for evaluating this predicted correspondence between habitat commonness and resident species richness. In addition to unimodal patterns, however, several studies have interpreted monotonic patterns of species richness along regional productivity gradients (Abrams 1995, Waide et al. 1999) and especially decreasing monotonic patterns in the case of herbaceous plant communities (Grace 1999). Hence, our analysis is not exclusive to the unimodal relationship.

Methods of analysis

As with any process or pattern involving evolutionary time, it is not possible to measure directly the relative amount of historical land area belonging to different habitat productivity types. It is possible, however, to estimate the contemporary relative frequency of different habitat productivity types recorded from vegetation surveys and then to analyze the distribution patterns of these estimates in relation to corresponding species richness patterns. We tested two hypotheses applied to published data sets: (1) habitats of intermediate productivity were more common than habitats of lower or higher productivity (the prediction for unimodal species richness patterns); and (2) habitats of low (or high) productivity were more common than habitats of higher (or lower) productivity (the prediction for monotonic species richness patterns). These hypotheses were not mutually exclusive, e.g. a right-skewed unimodal distribution could be considered as both unimodal and decreasing monotonic. In order to objectively test the relative commonness and rarity of data points (individual habitats) along the productivity gradient of each data set, we used Monte Carlo procedures (Manly 1991, Gotelli and Graves 1996). The advantage of these types of tests over other distribution tests is that they make no a priori prediction of the specific form of the distribution (unlike, for example, the Shapiro-Wilks test which tests specifically for normality, as opposed to unimodality).

Hypothesis 1 (unimodal patterns)

For each data set, we divided the habitat productivity distribution into three sections by ‘cutting’ the gradient at two points, each positioned randomly between the lowest and highest productivity values, inclusive (Fig. 1). We then counted the number of points (sites) falling within each section to create a frequency histogram of habitat productivity types consisting of three bars of random width. We repeated this random cutting and counting procedure for a total of 3000 iterations per data set, and thus obtained 3000 three-bar histograms. We considered data sets for which the middle histogram bar was the highest significantly more frequently than

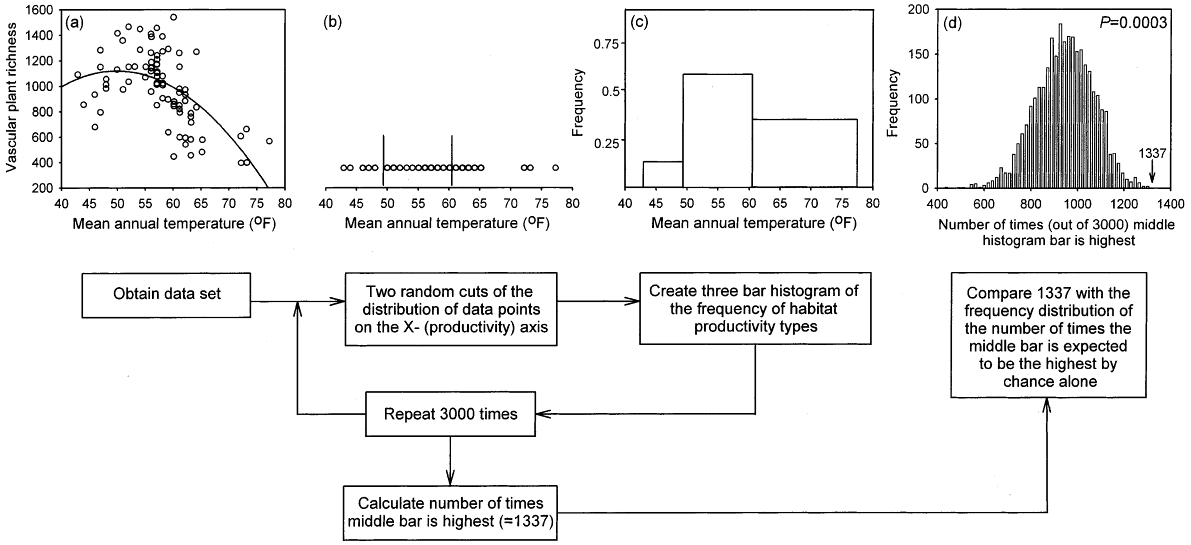

Fig. 1. Flow chart of the Monte Carlo procedure used to analyse potential unimodal distributions of habitat productivity types (hypothesis 1) for an example data set (Richerson and Lum 1980). For each data set (a), the axis of the independent variable (representing a gradient of habitat productivity types) was subjected to two random ‘cuts’, as indicated by the vertical lines in (b). Enumerating the number of points in the three sections of the distribution created by these cuts resulted in a three-bar histogram (c). This process was repeated 3000 times to determine the number of times that the middle bar of the histogram contained the most points. This quantity (1337 in the present example) was used as the test statistic for the Monte Carlo procedure, and was compared (arrow in (d)) against the distribution of test statistics generated by applying the cutting procedure to many (i.e. 3000) random data sets chosen from a uniform distribution (d). The resultant P-value indicated whether or not the middle bar was the highest more often than expected by chance alone, and hence, whether the distribution of habitat productivity types was considered to be unimodal (supported in this example; $P = 0.003$).

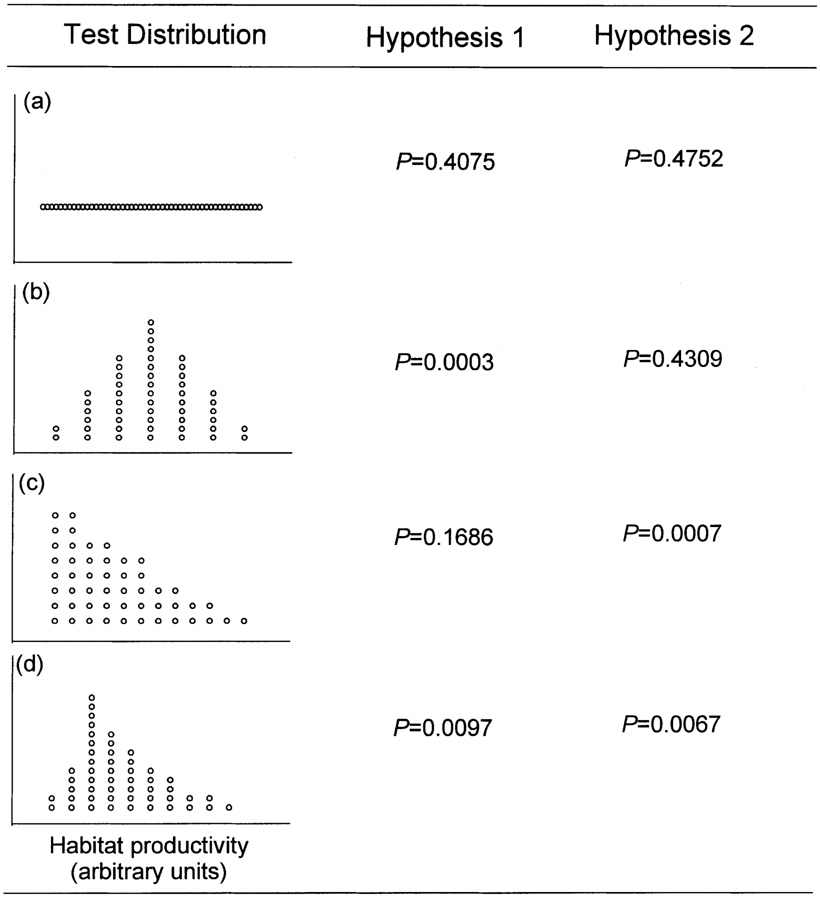

Fig. 2. Four artificial distributions used to test the efficacy of our methodology. The four 50-element test data sets were constructed to have uniform (a), unimodal (b), decreasing monotonic (c), and right-skewed unimodal (d) habitat productivity distributions (units arbitrary). Data points were projected along an arbitrary y-axis to more clearly depict the number of points associated with each x-value. The corresponding middle and right columns show the results (*P*-values) of the randomization tests for hypotheses 1 and 2 respectively applied to each distribution. See text.

expected by chance alone to have a unimodal habitat productivity frequency distribution (i.e. hypothesis 1 was supported). Thus, it was necessary to perform the above procedure on 3000 random data sets drawn from a uniform distribution to obtain a 3000-element distribution of the expected number of times (out of 3000) that the middle bar was the highest, in the absence of biases in the positions of habitats along the productivity gradient. Each random data set had 50 productivity values, regardless of the number of habitats present in the real data set being tested. While it would have been preferable to use the same number of productivity values as was present in each real data set, the necessary computing power was not available to us. However, since the height of the middle bar of each histogram was always determined relative to the height of the other two bars, there is no reason to expect that the absolute number of data points would bias, in any particular direction, the number of times the middle bar was the highest. Comparing the number of times out of 3000 that the middle bar from the real data set was the highest (our test statistic) to the distribution of the number of times out of 3000 that the middle bars from the 3000 random data sets were the highest (Fig. 1) allowed for the calculation of a two-tailed *P*-value (Manly 1991):

$$P = \min\,[(2S/3001), (2L/3001)]$$

(cf. Bersier and Sugihara 1997),

where S is the number of values in the random distribution equal to or smaller than the observed value and L is the number of values in the random distribution equal to or larger than the observed value. P of less than 0.05, combined with L less than S, indicated that the middle histogram bar was the highest significantly more of the time than expected by chance alone, and therefore that habitats of intermediate productivity were significantly more common than habitats of relatively low or high productivity.

Hypothesis 2 (monotonic patterns)

Here, we followed a procedure that was very similar to that of hypothesis 1 (above). The main difference was that instead of cutting the productivity distributions (for both real and random data sets) into three sections,

Table 1. Summary of results from testing hypotheses for unimodal and decreasing monotonic frequency distributions of habitat productivity types in 11 published studies.

Study	Reported species richness pattern	Relative productivity estimate	Spatial scale	*P*-values for unimodal habitat productivity type distribution (hypothesis 1)	*P*-values for decreasing monotonic habitat productivity type distribution (hypothesis 2)
Garcia et al. (1993)	Unimodal	standing crop/0.25 m^2	Regional	0.2609	0.0003
Gough et al. (1994)	Monotonic (–)	biomass/m^2	Regional	0.3549	0.0913
Grace and Jutila (1999)	Unimodal	biomass/m^2	Regional	0.0103*	0.0003
Huston (1980)	Monotonic (–)	soil fertility/0.1 ha	Regional	0.0073*	0.0003
Hutchinson et al. (1999)	Unimodal	N mineralization rate	Landscape	0.0233	0.0030
Moore and Keddy (1989)	Unimodal	standing crop/0.25 m^2	Regional	0.2086	0.0003
Richerson and Lum (1980)	Unimodal	Mean annual temp.	Regional	0.0003	0.1873
Shipley et al. (1991)	Unimodal	biomass/0.25 m^2	Regional	0.3476	0.0467
Vasander (1987)	Monotonic (–)	biomass/m^2	Regional	0.0003*	0.0003
Wheeler and Giller (1982)	Monotonic (–)	standing crop/0.25 m^2	Regional	0.4342	0.0003
Wheeler and Shaw (1991)	Monotonic (–)	standing crop/m^2	Regional	0.0387*	0.0003

* Because of the two tailed nature of this test, four cases of significant *P*-values represented distributions where intermediately productive habitats were less rather than more common than expected by chance. For each of these cases, however, there was a significant decreasing monotonic frequency distribution of habitat productivity types.

we cut them into two sections, giving two-bar histograms. The test statistic was the number of times out of 3000 that the left bar was higher than the right bar; as before, this was tested against the distribution of test statistics generated from 3000 random data sets. Thus, we were able to test the hypothesis that the distribution was monotonic, and if so, whether the distribution was increasing or decreasing monotonic. We calculated two-tailed *P*-values in an analogous fashion to the calculation of the *P*-values for hypothesis 1. Here, however, *P* of less than 0.05 combined with *L* less than *S*, indicated that habitats of relatively low productivity were significantly more common than habitats of relatively high productivity. Conversely, *P* of less than 0.05 combined with *L* greater than *S*, indicated the opposite, i.e. that habitats of relatively high productivity were significantly more common than habitats of relatively low productivity.

Test data sets

In order to assess the utility of our tests, we applied the above methods to four artificial data sets that we considered, a priori, to be uniform, unimodal, decreasing monotonic and right-skewed unimodal (Fig. 2). As expected, hypotheses 1 and 2 were both rejected for the uniform data set (Fig. 2a). For the unimodal data set, hypothesis 2 was rejected but hypothesis 1 was supported; i.e. habitats of intermediate productivity were more common than habitats of lower or higher productivity (Fig. 2b). In contrast, for the decreasing monotonic data set, hypothesis 1 was rejected but hypothesis 2 was supported; i.e. habitats of low productivity were more common than habitats of higher productivity (Fig. 2c). Finally, for the right-skewed unimodal data set, both hypotheses were supported (Fig. 2d).

Analyses of published data

The methods of analysis described above are based on the assumption that the distribution of habitat productivity types within a given data set is representative of the relative availability of those different habitat types in the landscape or region under study. Accordingly, in surveying the literature for suitable data sets for analysis, a study was not considered if the sites had been selected intentionally to equalize the representation of different habitat productivity types along the gradient. Our approach applies only to data sets in which the data points represent sites that were selected based on their availability without regard, a priori, for their relative productivity. We also selected only studies in which the gradient of productivity was considered to represent a gradient in the resource-supplying power (e.g. fertility) of the habitat. Studies of disturbance gradients were not considered; although the species pool hypothesis could also be applied to predict species richness patterns on disturbance gradients, we do not pursue this in the present analysis.

We obtained data from a total of 11 studies that satisfied the above criteria and reported a significant pattern of decreasing plant species richness toward the high end of a habitat productivity gradient (Table 1). Several different measures were used for estimating relative productivity in these studies (Table 1), but their relative merits are not considered here. Seven studies considered only herbaceous plant communities, one considered only tree species, and three studies considered both woody and herbaceous vegetation. Ten studies investigated richness-productivity relationships within single community types (i.e. only forests, only wetlands etc.) and one study spanned all plant community types within a large region (Richerson and Lum 1980). Community types in these studies included wetlands (Moore and Keddy 1989, Shipley et al. 1991, Gough et al. 1994), fens (Wheeler and Giller 1982, Wheeler and Shaw 1991), salt marshes (Garcia et al. 1993), grasslands (Grace and Jutila 1999), boreal mires (Vasander 1987), temperate forests (Hutchinson et al. 1999) and tropical forests (Huston 1980). Although only landscape and regional scale studies were chosen for our analysis, these studies ranged in scale from the examination of a number of wetlands within two watersheds (Gough et al. 1994) to the analysis of the entire state of California (Richerson and Lum 1980).

The species richness patterns reported were interpreted by the authors as unimodal in six of the studies and decreasing monotonic in the remaining five studies. In order to fully explore the implications of these methods of analysis, both hypotheses 1 and 2 were tested for each data set, although hypothesis 1 is designed for strictly unimodal patterns. Since all of the unimodal data sets were right-skewed, however, all of the data sets could be considered to have a general decreasing species richness pattern across most of the productivity gradient, consistent with the decreasing monotonic pattern of hypothesis 2.

The analyses revealed strong support for the species pool hypothesis. Four of the five studies considered to have a decreasing monotonic species richness pattern also had a significant decreasing monotonic habitat productivity type distribution (supporting hypothesis 2) (Table 1). Two of the studies regarded as showing a unimodal species richness pattern (Richerson and Lum 1980, Hutchinson et al. 1999) also had a significant unimodal habitat productivity type distribution (supporting hypothesis 1). However, all four of the remaining 'unimodal' studies involved right-skewed unimodal species richness patterns and hence, could also be regarded as having a decreasing monotonic species richness pattern. All four of these studies also had a significant decreasing monotonic habitat productivity type distribution. Hence, in every study except one (Gough et al. 1994) where the monotonic test (hypothesis 2) was not quite significant ($P = 0.0913$), the most productive habitat types were not only lower in species richness, but were also less common in the data set than habitat types of low and/or intermediate productivity, regardless of whether the data were interpreted as showing decreasing monotonic or unimodal species richness patterns (Table 1).

Discussion

Numerous studies have established what is now considered to be a common, widespread pattern in vegetation ecology: highly productive habitats typically have fewer resident species than habitats of very low or intermediate productivity (Grace 1999). These relationships are described as decreasing monotonic or unimodal, respectively. Much of the theory that has been proposed to explain this pattern involves interspecific competition as the principle mechanism; i.e. relatively low species richness in highly productive (fertile) habitats is considered to be a consequence of relatively intense competition in these habitats (which may also be modulated by variation in the level of disturbance) (Grime 1979, Huston 1979, 1994, Grace 1999, 2001). Although the evidence is controversial (e.g. see reviews by Gurevitch et al. 1992, Wilson and Lee 2000), several studies have indeed suggested that the competition intensity experienced by non-resident species (and hence, the competitive exclusion of these species) is more intense in highly productive habitats or under experimental conditions of relatively high resource availability or fertility, especially when there is low disturbance (e.g. see Bonser and Reader 1995, Gaudet and Keddy 1995, Twolan-Strutt and Keddy 1996, Keddy et al. 1997, 2000 and references cited there). Clearly then, this is an important mechanism for explaining why species richness is relatively low under conditions of high habitat productivity. However, this mechanism is only a proximal ecological one; it explains why some species are not adapted to highly productive habitats and thus do not reside there. It does not explain the principal reason for low species richness in these habitats; i.e. it does not explain why the adapted (i.e. resident) species in highly productive habitats are relatively few in number (Aarssen 2001). Moreover, the empirical evidence indicating competitive exclusion of a relatively large number of species from highly productive (fertile) habitats does not indicate that competition intensity is relatively high under these habitat conditions; rather, it just indicates that these species do not possess the necessary adaptations for effective competitive ability under these habitat conditions (Taylor et al. 1990).

The critical question in an evolutionary context, therefore, is not why are so many species (the non-residents) excluded from highly productive habitats, but rather, why are there so few species (the resident species) that are not excluded from these habitats? The species pool hypothesis addresses this question explicitly. The resident species of a habitat type are those that can successfully recruit offspring within the habitat and are, by definition, therefore, adapted to all of the environmental conditions that characterize the habitat, including the biotic conditions resulting from interspecific competition for limited resources. According to the species pool hypothesis, the resident species in highly productive habitats are relatively few in number because these habitat types have been relatively uncommon and, thus, have had relatively little historical opportunity, in space and/or time, for the origination of species that are adapted to the environmental conditions of highly productive habitats and, in particular, species with sufficient competitive ability under these habitat conditions (Taylor et al. 1990, Aarssen 2001). This model assumes, therefore, that if these historical speciation opportunities had not been limited in highly productive habitats, then neither would contemporary species richness be limited in these habitat types, even though competition is intense here (i.e. approaching equilibrium or carrying capacity) and even regardless of what opportunities may or may not exist for niche differentiation in these habitat types. Numerous mechanisms for promoting species coexistence within vegetation have been proposed that do not require avoidance or reduced intensity of competition through niche differentiation or disturbance (non-equilibrium) effects (see review by Bengtsson et al. 1994). One such mechanism predicts species coexistence as a consequence of an evolutionary disequilibrium, where effective competitive ability within a given habitat is defined by several alternative trait combinations possessed by several different species and genotypes within species that are all, therefore, able to avoid competitive exclusion despite intense competition (Aarssen and Keogh 2002). This coexistence mechanism has been referred to as "selection for competitive combining ability" (Aarssen 1983, 1989, 1992) and also, more recently by Hubbell (2001), as "zero sum ecological drift".

The role of species pools in regulating local diversity of vegetation has been explored in several studies over the past decade (see reviews by Zobel 1997, Grace 2001). Some studies have found that variation in small scale species richness between habitats differing in community biomass correlates well with estimates of the sizes of species pools associated with these community biomass types at larger, regional scales (e.g. Wisheu and Keddy 1996, Partel et al. 1996, 2000, Partel and Zobel 1999, Liira and Zobel 2000). Other studies by J. B. Grace and colleagues (see Grace 2001) have used structural equation modeling to search for correlations between abiotic environmental factors and patterns of diversity that are indicative of gradients in species pools. None of these previous studies, however, have tested the central prediction of the species pool hypothesis, i.e. the correspondence between the commonness of habitat types and the resident species richness of these habitat types along productivity gradients (Taylor et al. 1990). We were able to test this prediction using an approach based on Monte Carlo randomization procedures. Applying this approach to eleven published data sets, we found strong support for our prediction: highly productive habitats are generally less common than habitats of low and/or intermediate productivity, which, according to the species pool hypothesis, accounts for their relatively low species richness. A parallel interpretation of the role of habitat commonness in affecting species pool size has been applied recently to account for the scarcity of plant species that possess the biennial (compared to annual) life history (Viswanathan and Aarssen 2000).

The methods of analysis proposed here can be used with any data set in which study sites have been selected without bias in regard to their position on a productivity gradient, i.e. where the relative frequency of habitat productivity types sampled is representative of their actual relative frequency in the landscape. It is important to recognize, however, that this procedure allows only an indirect test of the species pool hypothesis; local/regional scale and contemporary habitat commonness are used in this approach as surrogates for global scale and historical habitat commonness, respectively. There will always be some uncertainty as to whether a selection of sites within a limited study area is representative of the full range of possible habitat productivity types available for supporting vegetation over larger spatial scales. Future studies may apply these methods to a wider range of data (e.g. as assembled recently by Mittelbach et al. 2001), including those that report an increasing species richness with increasing productivity.

These spatial scaling issues are particularly important in the assessment of how species richness varies across productivity gradients. Ecological determinants of species richness involving interspecific interactions (especially competition) act predominantly at local scales and should, therefore, be investigated at local scales (Huston 1999). The local species richness patterns generated by these processes influence regional species richness patterns when aggregated. However, regional processes, which may or may not act in the same way as local processes (Scheiner et al. 2000), are also important in determining regional-scale species richness patterns. These regional processes are dominated by evolutionary processes, such as speciation. The species pool hypothesis (as envisioned by Taylor et al. 1990) is an evolutionary hypothesis involving effects of historical patterns across habitat types in the origination of adapted species, and is most appropriately applied to regional species richness data. Hence, the competitive exclusion hypothesis (of the hump-backed model) and the species pool hypothesis should not be regarded as mutually exclusive; regional species richness patterns are likely to be a product of a complex interaction of local and regional processes.

Other methodological limitations are associated with difficulties in assessing the geological ages of different habitat productivity types and the extent to which their relative frequency distribution has changed over evolutionary time. Nevertheless, recent surveys involving detailed estimates of primary productivity of representative habitat types across landscapes (Brown and Schroeder 1999, Hansen et al. 2000) have reported unimodal frequency distributions consistent with the results of our analyses; i.e., highly productive habitats are relatively uncommon. In addition, we know that over most of the earth's surface, the most highly productive lands are presently under cultivation and this amounts to only a small percentage (about 11 percent in 1990) of the total ice-free land area in the world (Tolba et al. 1992). Even most of this 11 percent, although cultivated, has substrates with only relatively moderate natural fertility, thus often requiring the addition of commercial fertilizers.

This relative spatial rarity of extremely fertile habitats follows practically inevitably, we suggest, from the 'left wall' effect in generating a right-skewed unimodal distribution of habitat productivity types. The relative scarcity of resident species in these habitats is perhaps, therefore, no less inevitable and hence, explainable largely in terms of the restricted historical opportunity predicted for the origination of species that possess the adaptations, including competitive ability, necessary to leave descendants under these rare habitat conditions.

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Editor's note

Due to unforeseen difficulties with the mailing services resulting in the disappearance of edited manuscripts on the way from the Editorial Office to our printer, some of the papers printed in this issue were unnecessarily delayed. We wish to extend our apologies to the authors of Ehrlén et al., Carlsson-Granér and Thrall, Venzon et al., Goubitz et al. and Janssen et al. for this inconvenience.

Ed.