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Three competing models for predicting the size of species pools: a test using eastern North American wetlands

Irene C. Wisheu and Paul Keddy

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With growing emphasis on protecting biodiversity, there is an increasing need for models which can predict the size of species pools in different habitats. Three models make predictions of how the species pool should change along environmental gradients. First, the productivity model predicts that the largest species pools will occur at high productivity (or at high biomass in herbaceous systems). Next, the species pool model predicts that the largest species pools will occur at the same biomass level as highest alpha diversity (the number of species in a small sample of uniform habitat). Finally, centrifugal organization predicts that species pools will be largest where biomass is low. We tested the three models to determine which was most appropriate using biomass/species composition data from 33 eastern North American wetlands. The resulting 640 quadrats produced a pattern of pool size consistent with the species pool model. Both alpha diversity and the species pool were maximum at intermediate biomass levels. This suggests that (1) the processes of stress tolerance, disturbance tolerance, and competition that are associated with changes in alpha diversity may also influence the species pool, and (2) the more easily measured alpha diversity values can be used to predict where large species pools might occur.

I. C. Wisheu and P. Keddy, Dept of Biology, Univ. of Ottawa, P.O. Box 450, Station A, Ottawa, ON, Canada K1N 6N5 (present address of ICW: Dept of Biology, McGill Univ., 1205 Ave. Docteur Penfield, Montreal, QC, Canada H3A 1B1 (iwisheu@bio1.lan.mcgill.ca)).

Patterns of diversity are central in both the study of ecology and in the development of applications for biological conservation (May 1986). As befitting the importance of the subject, several books have recently been written on diversity (e.g. Ricklefs and Schluter 1993, Huston 1994, Rosenzweig 1995). These books highlight how many factors are associated with diversity and how many models have been proposed to account for variation in diversity along gradients. Several established models focus on predicting changes in alpha diversity, the diversity in small samples of uniform habitat (sensu Whittaker 1975; for example, models by Grime (1973, 1979), Connell (1978) and Huston (1979)). However, a new and more pressing challenge is to predict changes in biodiversity.

Biodiversity is the pool of species available to colonize a given habitat. The size of the species pool is believed to be determined by speciation and extinction rates (Wiens 1983) and by historical processes governing migration (Zobel 1992). It has therefore been suggested that extant species richness should be viewed as an artifact of past biogeographical and historical events rather than as a product of ecological opportunities (Cornell and Lawton 1992, Li and Adair 1994). However, there are few opportunities to test this view. Many of the questions regarding the species pool can only be

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addressed at the landscape scale, and few data sets exist at this large a scale. Nevertheless, models that make predictions of how species pools change along environmental gradients have been proposed.

There are at least three competing models in the literature that predict where large species pools will occur in relation to habitat biomass. The oldest model, the productivity model, states that there will be greater numbers of species with increasing productivity (Connell and Orias 1964; see also Southwood 1977, 1988). With increasing productivity, larger populations are supported and the populations tend to be sedentary. Since these larger populations also promote more frequent interspecific associations and contain greater genetic variability, speciation is favoured. Species diversity is therefore related to productivity in a non-decreasing relationship. Since productivity closely approximates biomass in herbaceous wetland vegetation subjected to winter dieback, this prediction can be translated in this system as larger species pools with increasing biomass.

Next, the species pool model (Taylor et al. 1990) predicts that the largest species pools will occur at lower biomass than the preceding model. The species pool should reach maximum size at the same biomass as the maximum of alpha diversity. Like the productivity model, this newer model also relates the size of the species pool to opportunities for speciation. The species pool model states that larger pools are a consequence of greater area and/or geological age of habitats (see also Eriksson 1993). However, by itself, this explanation is insufficient to explain why maximum alpha diversity and pool size should coincide. It is therefore implicit in the model that alpha diversity is a constant subset of the species pool. This idea is reminiscent of Preston's sampling hypothesis (Preston 1948, Cornell and Lawton 1992), which suggests that species assemblages are random samples drawn from a pool of potential colonists. The second model to be tested in this study is therefore a combination of Taylor et al. (1990) and Preston (1948), but will be referred to as the species pool model. The species pool model has not been previously tested (but see Pärtel et al. 1996).

Finally, the centrifugal organization model predicts that the species pool will be highest near the low end of the biomass gradient (Keddy 1990, Wisheu and Keddy 1992). Pool size is viewed as an artifact of habitat diversity, with there being more different kinds of low biomass habitats than high biomass habitats. As the number of habitats used to generate measurements of the species pool is increased, the size of the species pool will rise, primarily in low biomass habitats. Maximum pool size will not be coincident with maximum alpha diversity. To test among the three models predicting changes in the size of the species pool, we therefore needed to construct and then compare patterns of alpha diversity and pool size along a biomass gradient.

Methods

Species composition was recorded and biomass measurements were made in 33 eastern North American wetlands. The wetlands were in seven different geographic areas, areas defined on the basis of ecoclimatic region and drainage basin. Within each geographic area, wetlands were selected and sampled so that low, medium, and high biomass wetlands were represented. SYSTAT cluster analyses (SYSTAT 1990) were used to identify the wetlands as 33 distinct sites.

At each wetland, 0.25-m^2 quadrats were positioned within the zone of emergent marsh or wet meadow vegetation, below the shrub zone and above aquatic macrophytes. Quadrats were positioned to represent the full range of biomass values present at the wetland, with no fewer than 10 quadrats at each wetland site. From within the quadrats, all rooted vascular plant species were identified and all aboveground biomass was harvested, dried for at least 24 h at 60°C in a forced-air convection oven, and weighed to the nearest 0.01 g. The quadrats were sampled between 23 July and 1 October, intermittently from 1983 to 1992. In total, 640 quadrats were sampled from Ontario, eastern Quebec, and southern Nova Scotia, many of them as part of separate projects reported elsewhere (Day et al. 1988, Moore and Keddy 1989, Wisheu and Keddy 1989, Lee 1993, Gaudet and Keddy 1995).

To calculate the size of the species pool, quadrats were grouped together in a set, and then the total number of species in the set was counted. For example, in two quadrats with 5 species each, alpha diversity values would be 5 in each. But the species pool for the combined quadrats would range from 5 (if both quadrats had identical species) to 10 (if none of the species in the two quadrats were the same). That is,

$$P_{min} = \alpha_{max} \quad \text{and} \quad P_{max} = \Sigma^n \alpha$$

where P denotes the species pool and n is the number of quadrats grouped together in a set. Generating patterns of how the species pool changes along a biomass gradient therefore required that quadrats be grouped. We describe the grouping method in some detail because this is, to our knowledge, one of only a few attempts to relate species pool and alpha diversity measurements (Cornell 1985, Cornell and Lawton 1992, Kohn and Walsh 1994; but see Cresswell et al. 1995).

First, all quadrats from the 33 sites were ordered from lowest to highest biomass. Then, taking sets of 100 quadrats at a time (e.g. 100 with the lowest biomass), subsets of 50 quadrats were randomly drawn. (The random draws were made so that the quadrats represented exactly 9 different wetland sites from 6 of the 7 different geographic areas. This ensured that greater geographic diversity within some groups of quadrats would not artificially inflate the size of the species pool.) Then, for this subset of 50 quadrats, pool size was calculated, as well as average biomass and average alpha diversity. Next, from the same initial set of 100 quadrats, a second subset of 50 quadrats was randomly selected, and then the size of the pool, average biomass, and average alpha diversity values were re-calculated. Subsampling was repeated a total of 5 times, to estimate mean values of pool size and average alpha diversity for values of average biomass. This procedure generated a single point in each of the two graphs in Fig. 1. Finally, the whole procedure was repeated for other sets of 100 quadrats, shifted 20 quadrats up the biomass gradient each time.

Results

First consider the data on alpha diversity (Fig. 1, bottom). The range of biomass values extended from 0.37 to 1219 g per 0.25 m^2 and the range of alpha diversity values were from 1 to 24 species per quadrat. Maximum alpha diversity occurred in the range from 10 to 60 g/0.25 m^2, results consistent with predictions of intermediate diversity models (Grime 1973, 1979, Huston 1979). This range of biomass values is also consistent with the range reported to support maximum alpha richness in other eastern North American wetlands (Wilson and Keddy 1988, Shipley et al. 1991).

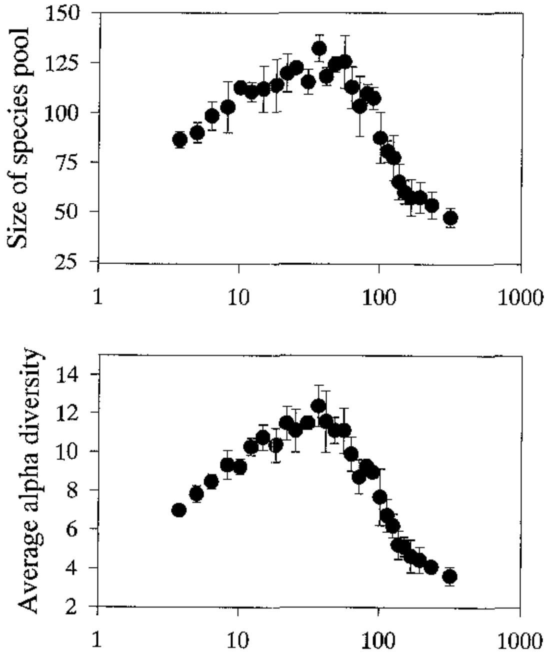

Fig. 1. The size of species pools (top) and average alpha diversity (bottom) plotted against the average biomass of wetland habitats. Each dot represents mean values calculated from five randomly selected sets of 50 quadrats each, with bars representing 95% C.I.'s of the means.

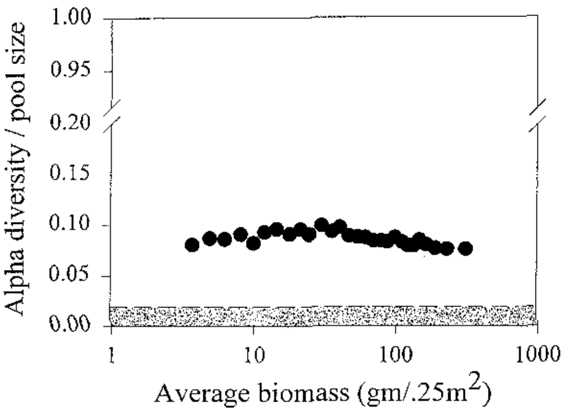

Fig. 2. The ratio of average alpha diversity to pool size plotted against the average biomass of wetland habitats. The shaded region is where values cannot occur when n = 50.

Now compare the pattern of alpha diversity to the size of the species pool. As predicted by the species pool hypothesis (Taylor et al. 1990), maximum pool size occurred at the same point along the biomass gradient as did maximum average alpha diversity (Fig. 1). At low to intermediate biomass (36 g/0.25 m^2), fifty quadrats contained an average total of 132 species. This contrasts with the lowest biomass levels (4 g/0.25 m^2), where fifty quadrats supported 87 different species and at the highest biomass levels (316 g/0.25 m^2) where fifty quadrats had only 47 species. For all points along the biomass gradient, alpha diversity represented a nearly constant fraction of the species pool (Fig. 2). In Fig. 2, the fraction is consistently 7–10%, but this value changes when species pools are generated using different numbers of quadrats (n not equal to 50) or different numbers of sites (Wisheu 1995).

Discussion

The patterns we observed are inconsistent with both the first model (productivity model) and the third model (centrifugal organization). Instead, the tight relationship between alpha diversity and pool size is consistent with the species pool model (Preston 1948, Taylor et al. 1990) which suggests that species assemblages are random samples drawn from a pool of potential colonists.

The species pool model

This study supports the species pool model but the mechanism of the model remains unclear. In the original explanation of the species pool model (Taylor et al. 1990), it was explicitly proposed that greater pool size is determined by greater opportunities for speciation, a function of greater geological age and/or global area. With this scenario, the well-known peak in alpha diversity at intermediate biomass is actually caused by the peak in pool size in this habitat type. This implies that alpha diversity is controlled through evolution rather than through ecological interactions.

An alternative (or complementary) view is that the species pool may itself be controlled, in part, by the very mechanisms (e.g. stress tolerance, disturbance tolerance, and competition) that have been proposed as controls on diversity within a quadrat (Grime 1973, 1979, Connell 1978, Huston 1979). These mechanisms may be operating at the evolutionary and biogeographic scales as well as at the quadrat scale. The distributions of stress-tolerant isoetids (Boston and Adams 1987) and competitive dominants (Gaudet and Keddy 1988) within the species pool indicate that competition and stress tolerance may be mechanisms operating within the species pool (Fig. 3).

While the mechanisms of tolerance and competition may play a role in determining the species pool, these mechanisms continue to be forces within communities. There are proportionally more isoetids in low biomass quadrats and more competitive dominants in high biomass quadrats than a random subsample of the pool would dictate (Fig. 4). These two groups of species are therefore responding to the environment, indicating that community composition is not solely an artifact of random sampling. As species colonize, some species appear to be favoured by the environment and are therefore more frequent in the community. Other species may colonize but occur infrequently. Alpha diversity remains a constant fraction of the species pool, with environmental factors apparently influencing which species are chosen from the species pool.

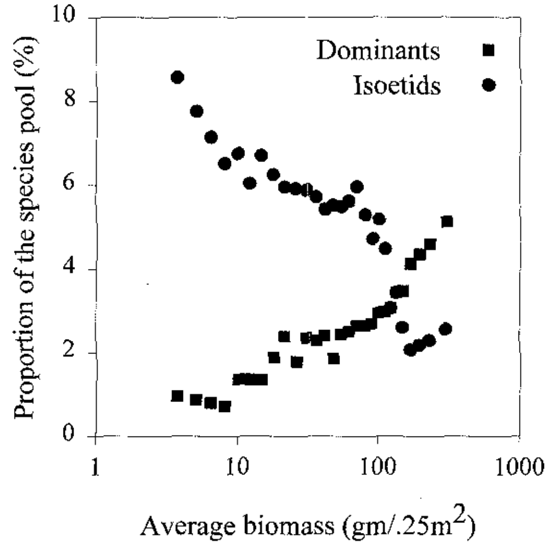

Fig. 3. Stress-tolerant isoetids (circles) and competitive dominants (squares) expressed as proportion of the species pool and plotted against the average biomass of wetland habitats. The ten isoetid species are from a list by Boston and Adams (1987), the five competitive dominants are those identified by Gaudet and Keddy (1988) as having the highest competitive abilities of 44 wetland species. Species pools were generated using 100 quadrats at a time.

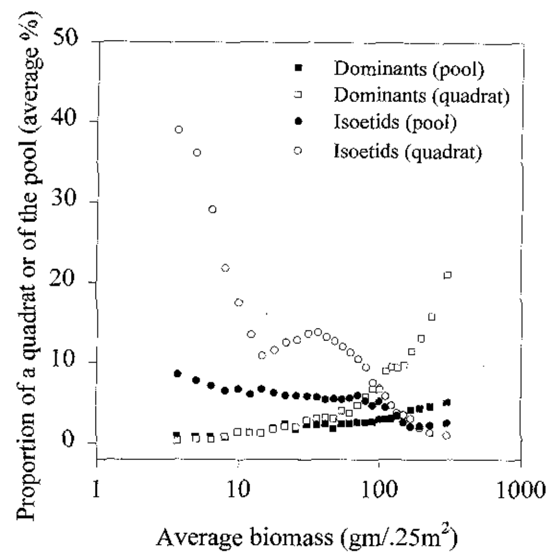

Fig. 4. Stress-tolerant isoetids (circles) and competitive dominants (squares) expressed as proportions of either quadrats or the species pool and plotted against the average biomass of wetland habitats. The species are as described in Fig. 3. Light symbols are averages of 100 quadrats. Dark symbols were calculated using 100 quadrats at a time.

There are important conservation implications to the species pool model. First, because there is a constant relationship between alpha diversity and pool size, the more easily measured alpha diversity value can be used to estimate the size of the species pool. Second, it is now possible to predict how species pools will change from one habitat to the next. For example, the preservation of low biomass wetlands will protect a larger species pool than the preservation of high biomass wetlands.

Alternative models

Since the centrifugal organization model failed to predict how the size of species pools changed along the biomass gradient, then either the centrifugal organization model is wrong or there are problems with our deduction of predictions that are consistent with the model (Keddy 1990, Wisheu and Keddy 1992). We suspect that the centrifugal organization model may represent a limiting case where competitive dominants successfully exclude subordinates to peripheral low biomass habitats (see also Ellenberg 1988). If this process is less than complete or weak, then subordinates may invade into higher biomass sites with sufficient frequency to regularly occur in species pools well away from peripheral habitats. Such species may illustrate the failure of competitive exclusion to create tight distributional limits along the biomass gradient. The centrifugal organization model should not yet be discarded as inappropriate, but may be considered as a limiting case in situations with strong competitive exclusion.

The productivity model also failed to predict patterns in the sizes of species pools in eastern North American wetlands, yet this model has previously proven successful using North American trees (Currie and Paquin 1987). We can only speculate that the differing results may be due to (1) the consideration of an entire flora versus a dominant growth form, (2) the lengths of the productivity gradients and the ensuing effects of scale (Wright et al. 1993), i.e., an east-west array of wetland sites versus a longer north-south gradient of tree diversity, or (3), the nature of the productivity gradients. The wetland gradient is probably a gradient of nutrient or light availability (a resource gradient sensu Austin and Smith 1989). The gradient in Currie and Paquin (1987) is a gradient of annual evapotranspiration, probably related to temperature (a regulator gradient, Austin and Smith 1989). When species are distributed along resource gradients such as nutrient or light availability, competition will occur and some species will be excluded, even if (or especially when) some resources are in high supply. When species are distributed along regulator gradients such as temperature, competition may not occur and a greater number of species may coexist (Austin and Smith 1989). Further testing of both the species pool model and the productivity model may determine when each of the two models is appropriate.

There is still much to be resolved regarding patterns of diversity but we now have one more tool for predicting where centres of biodiversity might occur. By using the species pool model and the intermediate diversity models (Grime 1973, 1979, Connell 1978, Huston 1979), we can now predict how alpha diversity and the species pool will change along biomass gradients. Since patterns of alpha diversity and pool size parallel each other, at least in this case, the more easily measured alpha diversity value might be used to predict maximum biodiversity. While the applicability of this relationship in other systems remains to be explored, we now know that for wetlands in eastern North America, protecting the low-intermediate biomass wetlands with high alpha diversity will protect large species pools as well.

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