

# The relationship between diversity and productivity in plant communities: facts and artefacts

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Once ecologists have found patterns in nature they are able to generate testable explanatory theories (Weiner 1995). One such commonly found pattern is that when exploring an environmental gradient, the relationship between plant species richness and above-ground biomass tends to be unimodal. This trend was first described by Al-Mufti *et al.* (1977), although only 14 sample plots were used, and the curve was fitted by hand. Despite the small data set and the rudimentary quantitative analysis used, this study formed the basis for an intuitive, conceptual model that explained the hump-backed curve of diversity in terms of influences by 'stress', disturbance and competition (Grime 1979).

More rigorous calculation tools (*sensu* Loehle in Weiner 1995) applied to larger data sets have allowed subsequent authors to explore the relationship further. For example, in many cases a second order polynomial regression has been found to fit significantly the unimodal relationship (e.g. Moore & Keddy 1989; García *et al.* 1993). However, this tool has been criticised because its lack of appropriate parameters means that can predict but not explain the relationship, and the beta response function has been proposed alternatively (Oksanen 1996). Unfortunately the beta response function fitted the data set of Al-Mufti *et al.* (1977) less well than did the polynomial model, and Oksanen (1996) was unable to explain the relationship in terms of abiotic and biotic stresses, as he had expected. Instead, he developed a third (no-interaction) model which shows that it is possible that 'a humped diversity curve . . . is produced as a scaling artefact'.

Oksanen (1996) raises an interesting point in warning about the need to consider the effects of plant size and small quadrats when interpreting an obtained unimodal curve. If plants are larger in more productive environments and the quadrat size is fixed and small, fewer individuals and (all else being equal) fewer species will be recorded. In fact, this is one of the six hypotheses proposed by Abrams (1995) to explain, without involving competition, the unimodal diversity curve. However, Oksanen (1996) goes further and, on the basis of simple (but unrealistic) assumptions, challenges any ecological explanation for the humped diversity curves. There are two weak points in Oksanen's argument: first, the unjustified

step from a pattern of plant density in monoculture to a trend of diversity in species mixtures. Along a productivity gradient, plants do not 'retain their shape', rather there is a vast array of shapes and growth forms and species turnover, and the increasing community biomass may or may not be associated with fewer plants per plot. The effect of plot size could be better ascertained by a sampling design with varying quadrat sizes and subsequent statistical analyses. Secondly, the parameter alpha (diversity), which links species number and plant number, is rarely, if ever, constant along an environmental gradient. For example, in our study of productivity in a saltmarsh (García *et al.* 1993) the communities of high biomass and low diversity (sedge lagoons) have much lower alpha values than the low biomass and highly diverse communities (upper saltmarsh grasslands).

The matter of scale is relevant, not only because of the chosen quadrat size and the possible distorting effect of plant size but also because the relationship between observed diversity and productivity may differ with the width of the gradient explored. Moore & Keddy (1989) described an unimodal diversity curve when a range of Canadian wetland communities were analysed together, but found no such significant relationship within individual habitats where biomass ranges were more limited.

The relative importance of competitive exclusion and environmental factors in accounting for the apparent decline of species richness in communities of higher biomass is much debated. For instance, abiotic factors such as soil salinity (García *et al.* 1993) and flooding depth (Gough *et al.* 1994) significantly and strongly reduce species richness but do not affect community biomass. In these harsh conditions many plant species are filtered out but the remaining, tolerant plants may attain a high biomass. Salinity and flooding do therefore influence species richness and community biomass (irrespective of the plot size), and much insight can be gained dissecting the separate response of such community parameters to environmental factors.

The search for patterns of diversity and the predictive values of environmental variables are also important tools for conservation managers. In a study of heathlands Ojeda *et al.* (1995) found that habitats at intermediate levels of the gradient were more species-

rich (since number of shrub species intercepted by a 100 m line was used as the measure of diversity it is unlikely that the resulting pattern was affected by plot size), and suggested that such sites should therefore have priority for conservation. Other biodiversity parameters (e.g. endemic species richness and taxonomic singularity) may, of course, point out to the need to conserve sites at other stages of the gradient.

Rosenzweig & Abramsky (1993) offered up to nine hypotheses to explain the productivity-diversity relationship. A tenth alternative, Oksanen's non-interaction model, should also be considered in future, if only to rule out the possibility of artefacts.

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Received 17 June 1996

revised version accepted 30 July 1996