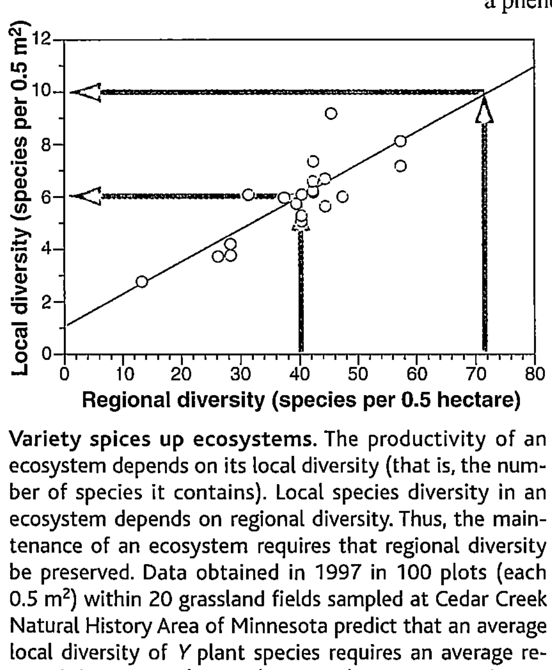
Diversity and Production in European Grasslands

David Tilman

The hypothesis that biodiversity influences the productivity (that is, the rate of biomass production) and stability of ecosystems has recently resurfaced (*1–3*), but it remains contentious (*4–6*). It is unclear whether the purported effect of species diversity on ecosystem productivity is actually the hidden signature of a few important species or whether it implies that species composition is less important than previously thought. Indeed, how can species diversity influence the functioning of an ecosystem, and do such processes operate in nature? Interest in these questions is particularly pertinent given the unprecedented extinction of many species and the reduction in diversity of myriad ecosystems wrought by human actions. On page 1123 of this issue, Hector and 33 European collaborators (*7*) report findings from a unique trans-European study of the effects of plant diversity on grassland productivity that provide answers to some of these questions.



Variety spices up ecosystems. The productivity of an ecosystem depends on its local diversity (that is, the number of species it contains). Local species diversity in an ecosystem depends on regional diversity. Thus, the maintenance of an ecosystem requires that regional diversity be preserved. Data obtained in 1997 in 100 plots (each 0.5 m^2) within 20 grassland fields sampled at Cedar Creek Natural History Area of Minnesota predict that an average local diversity of Y plant species requires an average regional diversity of $(Y - 1.1)/0.124$. (Regression analysis: $r = 0.82$, $n = 20$, $P < 0.001$). For example, a region must contain 40 species for a local site to contain 6 species.

Two mechanisms emerge as potential explanations for the effects of species diversity on productivity. The first, the sampling effect model, is based on the greater probability (given random species selection) that a species will be present when diversity is higher. If those species that are more productive in monoculture (that is, when growing on their own) are also better competitors than less productive species, then plots that are very diverse are likely to be more productive on average simply because of a greater chance of containing such competitive species (*5, 8*). A signature of the sampling effect is that no higher diversity plot should be more productive than the most productive species growing in monoculture. An alternative mechanism is based on niche complementarity (*8, 9*). These models predict that differences among species in resource or environmental requirements would allow some combinations of species to more completely capture and use resources and thus have greater productivity than any individual species in monoculture, a phenomenon called overyielding (*10*).

Several recent papers have explored these mechanisms with the use of theory, laboratory experiments, and a few field studies (*11*). To these can now be added the trans-European study of Hector *et al.*—the first large-scale, multinational field experiment of its kind in ecology (*7*). The investigators report results from its first 2 years. By experimentally controlling grassland diversity, they observed that loss of diversity led to significant decreases in productivity, similar to the findings of other field experiments. Most importantly, and quite surprisingly, across eight different European sites ranging from Sweden in the north, to Portugal and Ireland in the west, to Greece in the south and east, there seemed to be a "single general relationship between species richness and diversity across all sites" (*7*). Such broad inference is rare indeed in ecology. This landmark study demonstrates the power of multisite experiments and, perhaps, the power of a diverse team of scientists. Such experiments are critically important for addressing the effects of human domination on ecosystems and the benefits that ecosystems provide to society. The European Commission's funding of this project may herald the European Union's expanding interest in environmental science.

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Hector and collaborators found a strong effect of diversity on productivity and evidence suggestive of a simultaneous effect of composition on productivity. They did not find the pattern of species dominance and competitive displacement predicted by the sampling effect model but did find evidence of overyielding. Their results suggest a rule of thumb—that each halving of diversity leads to a 10 to 20% reduction in productivity. Could an ecosystem manager avoid this reduction by choosing the right species—such as those that are most productive in monoculture? Inspection of Fig. 2 in the Hector *et al.* paper shows that, in total across all sites, there were about 23 higher diversity plots that had greater productivity than the most productive monoculture at a site. This suggests that even the best monoculture may not equal many higher diversity plots. These results further support a niche complementarity model, although the mechanisms underlying such a model are still to be identified and only long-term studies can adequately address this issue.

How much diversity might be needed to maintain high productivity within an ecosystem? The answer requires some explanation. The trans-European experiment was performed in 2 m by 2 m plots. This is an appropriate size for determining how diversity influences productivity, because the effects of diversity must come from interactions among individuals of different species. In grasslands, individual species interact within an area of about 1 m^2. To apply these results to larger scales, it is necessary to know the regional diversity needed to attain a given level of local diversity.

The species-area relationship, $S = cA^z$, states that diversity, S, scales as area, A, raised to the power z, where z ranges from 0.15 to 0.3 (*12*). Consider a local area of size A_L and a region of size A_R. For the local area to have a local diversity of S_L species, the larger region would have to have $S_R = S_L (A_R/A_L)^z$. If one were to manage 100 hectares (1 km^2) to maintain high productivity, the work of Hector and colleagues suggests that each 1 m^2 should contain about 16 species. With $z = 0.15$, a 100-hectare field would have to contain 127 species for this to occur. Comparably, in Minnesota grasslands, we have observed a close relationship between the average diversity of 0.5-m^2 plots and the diversity of the 0.5-hectare region in which they occur (see the figure). Extrapolation with this relationship predicts that a 0.5-hectare region has to contain an average of 120 species for an average 0.5-m^2 site to contain 16 species (which implies a z value of 0.21). If about 16 species must occur in a 1-m^2 neighborhood to attain high productivity, z values ranging from 0.15 to 0.21 would predict that a single hectare would have to contain about 60 to 105 plant species and 1 km^2 about 127 to 270 species for high productivity to exist. Such values are similar to the plant diversity of many natural ecosystems but greatly exceed that of many managed ecosystems. This suggests that increasing diversity in managed grasslands and forests may be cost-effective.

The first 2 years of the trans-European study have provided important insights into the effects of species diversity on ecosystems. However, many controversies, such as the effects of diversity on stability and the mechanisms whereby diversity impacts productivity, are likely to remain unresolved until more years of data are gathered.

References and Notes

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11. See (*2–9*) and papers cited therein.
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