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Opinion is intended to facilitate communication between reader and author and reader and reader. Comments, viewpoints or suggestions arising from published papers are welcome. Discussion and debate about important issues in ecology, e.g. theory or terminology, may also be included. Contributions should be as precise as possible and references should be kept to a minimum. A summary is not required.

Distinguishing between the effects of species diversity and species composition

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Aarssen (1997) raises an important point, with which I agree – that interspecific differences in productivity, combined with the greater probability of having a productive species present in a high diversity plot, may cause productivity to increase with diversity. However, contrary to Aarssen's assertion, this does not mean that the relationship between diversity and productivity reported in Tilman et al. (1996) is an artifact. Rather, three interrelated phenomena – the effects of species diversity, the effects of species composition, and the reasons why diversity or composition have such effects – are being confused.

Ecologists have long known that ecosystem processes depend on species composition. Moreover, recent theory has shown that the effects of species diversity should depend on the magnitude of interspecific differences in such traits as resource use efficiency or productivity (Tilman et al. 1997). How, though, can the effects of changes in composition be separated from those of diversity? Deleting a single species from a community in a well-replicated experiment might seem to provide unambiguous information on the effects of species composition, but such a treatment also involves a change in diversity. Similarly, adding a particular species or set of species to a community involves changes both in composition and diversity.

To separate these requires replication and randomization that assures the species compositions are unbiased by species diversity, and vice versa. Specifically, given a group of all potential species, called the "species pool", for effects to be attributed to species diversity, they must occur in comparisons of the average response of two or more levels of diversity. Each level of diversity must include numerous replicate ecosystems that have random and independent combinations of species chosen from the species pool. These random species combinations assure that the mean response among replicate ecosystems at a given level of diversity is independent of particular species combinations. The differences among mean responses for different levels of diversity then unavoidably measure the effect of diversity. This is the approach used in the design of our diversity experiment (Tilman et al. 1996). This approach means that the significant differences in productivity, nutrient use and leaching that we observed are caused by diversity. However, this does not indicate why increased plant diversity caused productivity and nutrient use to increase. Aarssen (1997) proposed an interesting, important and simple mechanism that might explain why diversity had this effect. We independently developed this idea in a recently published paper that also presented two additional theories (Tilman et al. 1997).

All three of our models predicted that productivity and nutrient use would increase with diversity. Our simplest model, which we called the sampling effect, was the analytical embodiment of the same ideas that Aarssen (1997) discusses. It showed productivity was predicted to be an asymptotically increasing function of diversity, not the linear function suggested by Aarssen. The other models showed that resource use complementarity and niche complementarity led to similar effects.

In total, our experimental design (Tilman et al. 1996) controlled for the effects of species composition and revealed the effects of species diversity on productivity and nutrient levels, but additional information is needed to determine why diversity had the effects observed.

References

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