

another is an abdication of our obligation and responsibility to the patient.

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## Does diversity beget stability?

SIR — Tilman and Downing<sup>1</sup> present data which they argue support the hypothesis that more diverse plant communities are more stable. This finding, if well founded, would shed light on long-standing questions about the relationship between the diversity and stability of ecological communities<sup>2-4</sup>, and provide added motivation to conserve biological diversity. But this finding may be premature.

Tilman and Downing studied grasslands that developed different levels of vascular plant species richness (number of species per 0.3 m<sup>2</sup>) largely as a result of different amounts of nitrogen fertilization. Fertilization decreases species richness in this system<sup>5</sup>, paralleling a general tendency for grassland diversity to decrease with increasing soil fertility<sup>6,7</sup>. Community stability in response to drought was measured using the proportional rate of change in total above-ground biomass ( $1/B \times dB/dt$ ), estimated from the logarithm of the ratio of single harvests in successive years. More diverse quadrats showed greater resistance to drought, with less reduction in *B* heading into the drought year 1988; and greater resilience to drought, with faster recovery in *B* after 1988.

As expected from various economic models<sup>8-10</sup>, greater soil fertility generally favours plants with lower allocation to roots versus leaves, higher stomatal con-

ductance, and greater photosynthetic capacity. But plants with low allocation to roots and high stomatal conductance usually have low drought resistance, and plants with high photosynthetic capacity often do. Hence, the fact that quadrats with low species richness had the greatest drop in above-ground biomass during the 1988 drought may be a result of such quadrats having been those most heavily fertilized, and consequently those most likely to be dominated by drought-sensitive plants. The correlation of community resistance to drought and species richness may thus be illusory, reflecting the indirect effects of high soil fertility (in promoting drought-sensitive species or phenotypes) more than the effects of low diversity itself. A similar argument might apply to community resilience, which increased with species richness<sup>1</sup>. Plants adapted to low-diversity, high-fertility sites may have been most damaged by drought, and hence the slowest to recover.

Tilman and Downing<sup>1</sup> did attempt to control for possible shifts in the functional groupings of plants caused by shifts in soil fertility along their 'diversity' gradient by examining partial correlations of resistance and resilience with the number and abundance of C4 versus C3 species. But C4 grasses comprise only a small fraction of species richness in Tilman's experimental grasslands<sup>5</sup>, and controlling for their abundance would not screen effectively for systematic shifts in other drought adaptations along the fertility gradient. Furthermore, given that diversity and nitrogen levels are so closely related across plots<sup>5,10</sup>, it seems highly probable that some within-plot (among-quadrat) variation in diversity is tied to within-plot variation in nitrogen levels and root:shoot ratio; the latter were not measured. Thus, attempts to control for among-plot differences in nitrogen, C3 versus C4 abundance, or 1993 root:shoot ratios (see reply from Tilman *et al.*) are unlikely to eliminate completely the confounding effects of fertility on drought sensitivity.

Some of the variation in species richness among the Tilman-Downing plots reflects a difference in successional age: older fields tend to be more diverse<sup>5,10</sup>. These older, more diverse fields are known to be dominated by plants with a higher root:shoot ratio than those seen in younger fields<sup>10,11</sup> (perhaps reflecting more intense competition for nutrients in older fields), which may account for some additional portion of the apparent correlation between stability and diversity.

The underlying problem in the Tilman-Downing study is that diversity, community biomass, soil fertility, and (presumably) species sensitivity to drought are inter-correlated along the experimental gradient. It will require considerable in-

genuity to overcome this problem. One approach would be to select several random subsets including 2, 3, . . . ,  $n$  species drawn from a large species pool, sow these under a specific set of ecological conditions, allow community assembly (and potential species loss) to occur, and then measure community resistance and resilience. It would be even better to conduct such an experiment at several sites along climatic and edaphic gradients. Only by breaking down the correlations among diversity, community biomass, climate, edaphic conditions and plant adaptations can we determine whether species richness *per se* is an important determinant of community stability in biomass.

There are plausible arguments for either an increase in stability with diversity (such as greater numbers of functionally interchangeable species or species groups, each susceptible to slightly different perturbations; greater segregation of species into compartments that interact little, if at all) or a decrease in stability with diversity (for example, closer packing of competitors along resource spectra, evolution of species-specific mutualisms in diverse tropical habitats, time lags imposed by more trophic levels). It thus seems likely that diversity and stability (particularly with regard to species composition, as opposed to total biomass) may be related positively in some landscapes, and negatively in others.

It may yet be shown that the observed correlation of stability and diversity in the Tilman-Downing study is causal; there are many reasons why, under a fixed set of conditions, assemblages of 2 or 3 grassland species might be less resistant or resilient to disturbance than sets of 15 or 20 species. But even if the Tilman-Downing finding proves to be an artefact of adaptive shifts induced by fertilization and/or succession, it would have no bearing on the fundamental need to conserve biological diversity. Even if more diverse ecosystems were inherently more fragile to perturbation<sup>3</sup>, the agricultural, medical, scientific, economic and aesthetic values of biological diversity would still make the conservation of native species, communities, and ecosystems one of the world's most urgent priorities.

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**TILMAN ET AL. REPLY** — There are few long-term ecological studies of biodiversity, and even fewer that encompass a major natural disturbance. Our 12-year study<sup>1,5,12</sup> of 207 permanent grassland plots thus provides a unique record of the relationships between biodiversity and the stability of ecosystem productivity in response to drought. Givnish suggests that the strong relationship that we observed<sup>1</sup>

between ecosystem stability and plant species richness might be an artefact caused by changes in root-to-shoot ratios and photosynthetic physiology associated with nitrogen treatments. Because we had similar concerns about collinear variables when we began our analyses, we used multiple regressions to control statistically for effects of over 20 variables<sup>1</sup>. Whether we controlled for all of these simultaneously, one at a time, or in various combinations, there remained in all cases a highly significant effect of plant species richness (biodiversity) on ecosystem stability<sup>1</sup>.

Although we did not originally control for root:shoot-ratio shifts, we did measure root:shoot ratios in all plots in 1987 at the start of the drought (RSR<sub>1987</sub>) and in 1993 (RSR<sub>1993</sub>), by which time plots had returned to pre-drought biomass and composition. When we include RSR<sub>1987</sub>, RSR<sub>1993</sub> and their interaction (product of RSR<sub>1987</sub> and RSR<sub>1993</sub>) as additional covariates in backwards elimination multiple regressions, we find that part of the dependence of drought resistance on biodiversity is explained by 1993 root:shoot ratios ( $F=4.85$ ,  $P=0.03$ ), as Givnish suggests. The effect is in the right direction, but small (the overall  $R^2$  increases from 0.48 to 0.50). But contrary to Givnish's suggestion, the addition of root:shoot ratios does not eliminate, but rather slightly strengthens, the effect of biodiversity ( $F$  increases from 19.25 to 22.53;  $P<0.001$  for both). RSR<sub>1987</sub> and the interaction term do not significantly contribute to the multiple regression ( $F=0.01$ ,  $P=0.92$  and  $F=0.25$ ,  $P=0.62$  respectively).

In response to Givnish's concerns, we have performed other analyses that include root mass, changes in root mass,  $\log_e(\text{root mass})$ ,  $\log_e(\text{total biomass})$ , biomass of additional plant species, and various interaction terms as additional

covariates. In not a single case did the addition of any covariates eliminate the significant residual effect of biodiversity on stability. Thus we doubt if other physiological shifts, as suggested by Givnish, would eliminate the effects of biodiversity on ecosystem stability. Although no single study can eliminate all reasonable doubts about ecosystem functioning, the preponderance of available evidence<sup>1,13-17</sup> supports the hypothesis that biodiversity influences ecosystem functioning.

We agree with Givnish's proposal that a cleaner test of the effects of biodiversity on ecosystem functioning would come from direct experimental control of species diversity. In 1993 we began such a study. This 23-acre experiment includes 342 large (13 × 13m) and 147 small (3 × 3m) plots that contain 1-32 species randomly drawn from a pool of native prairie plants. These plots are being sampled to determine the effects of plant diversity on plant productivity, insects, plant pathogens, pollinators, and soil carbon and nitrogen.

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