Biodiversity and Ecosystem Properties

Because the goal of ecology is to understand the causes of patterns observed in the natural world, studies that document novel patterns in natural ecosystems are of central importance. The report "The influence of island area on ecosystem properties" by David A. Wardle *et al.* (29 Aug., p. 1296) is such a study. Some interpretations of data made by Wardle *et al.* illustrate the difficulty of ascribing causation on the basis of observation. In particular, their assertions "that ecosystem process rates were lowest on those islands with the greatest diversity" and that "this finding is in direct contrast to other studies which have shown elevated process rates in more diverse communities" are difficult to justify given their analyses and the data in the other studies (*1-4*).

In the archipelago studied by Wardle *et al.*, the variables of island size, fire frequency, successional state, and species composition were strongly interdependent. Compared with larger islands, smaller islands were found to have lower fire frequencies, higher plant diversity, and species compositions biased toward later successional species. Because of these interdependencies, correlations between any one of these variables and any of the ecosystem response variables may lead one to spurious conclusions. Multiple regressions, or other multivariate techniques, would be needed to determine if the data support the hypothesis that a given ecosystem response variable significantly depends on diversity, or composition, or fire frequency. Once there has been statistical control for correlations among these variables. Even when done carefully, such analyses of patterns in natural systems are still open to alternative interpretations.

Such difficulties have caused ecology to become an increasingly experimental science. Direct experimental tests of the effects of plant diversity on ecosystem properties (*1-4*) may give more valid results than would correlations that are uncorrected for collinear variables. The most significant advances come when results of experiments, observational studies, and theory (*5*) are congruent. Wardle *et al.* do not mention some aspects of these diversity experiments. All have found that plant species diversity or plant functional diversity, or both, have significant effects on ecosystem variables, but some of these rates were highest (*1-3*) and some were lowest (*3, 4*) in habitats with high diversity, and some seemed to vary idiosyncratically with diversity (*1*). In particular, there were lower soil concentrations of nitrate and ammonium in habitats with higher diversity (*3, 4*), which, contrary to statements by Wardle *et al.*, is consistent with the correlation they report.

We commend Wardle *et al.* on identifying a natural system that may provide significant insights into the forces controlling the functioning of ecosystems, but suggest that more complex analyses and experimental manipulations are needed to obtain the deeper insights that this system may offer.

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Response: The island system that we considered included islands with high plant diversity and those with low diversity. If plant diversity was an important causative agent for maintaining ecosystem properties in nature, then we would expect measurements of these properties to be greatest on islands with the greatest diversity. This was not the case, whether or not we analyzed the data by multivariate and multiple regression approaches correcting for the effects of island area and species composition. Although the patterns that we observed cannot be explained in terms of diversity effects, they can in terms of plant compositional effects and in particular the ecophysiological traits of the dominant plant species present. Our results are consistent with studies that found (i) little evidence in nature for consistent positive relationships between species diversity and ecosystem properties (*1*), (ii) idiosyncratic relationships between plant diversity and the functioning of decomposition-related processes (*2*), and (iii) plant physiological attributes to be important in determining ecosystem-level properties (*3*).

Tilman *et al.* state that we "do not mention some aspects" of previous diversity experiments and cite several references (*4-7*), but two of those (*4*) were not published until after our report was accepted. The other studies (*5-7*) found greater rates of processes in the highest diversity treatments for the majority of ecosystem properties that showed significant treatment responses. It is presumably those findings that induced Tilman *et al.* (*5*, p. 720) to conclude that reduced biodiversity "threaten ecosystem productivity and the sustainability of nutrient cycling" and Naeem *et al.* (*6*, p. 735) to state that loss of biodiversity will "alter *or impair* the services that ecosystems provide" [italics ours]. Our data are not in agreement with those findings, which are based on experiments in which the most diverse treatments may have a greater probability of being dominated by the most productive species in the entire species pool (*8*). Our results are in much closer agreement with recent studies (*4*) which are designed more robustly and are less likely to be influenced by this problem; these studies conclude that species composition, rather than species diversity, is the main determinant of ecosystem properties.

The data about mineral N presented by Tilman *et al.* (*5*) are not comparable with our data. In their study, the reduction of soil mineral N in the most species-diverse plots was presumably a result of the enhanced rate of a key process (plant productivity) that led to more complete N uptake. In our study, accumulation of organic N in the soil of the most species-diverse islands was induced by retardation of key soil processes and resulted in long-term lock-up of N in biologically inaccessible pools.

We agree with Tilman *et al.* about the utility of experimental and theoretical approaches and in this light have recently established long-term manipulative experiments on our island system. One experiment, initiated in 1996, aims to determine the ecosystem-level significance of both plant species and functional group diversity across 30 of our islands; it includes the use of 420 experimental plots. We believe, however, that experimental and theoretical approaches are only a means to an end (the end being to better understand what happens in real ecosystems) rather than an end in themselves. We are not persuaded that experimental tests should have precedence, and believe that if outcomes of short-term experimental (*5*,*6*) and theoretical studies do not concur with patterns and processes observed in nature (*1* and our report), then it is the experiments and theory that should be queried.

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