# Commentary

# An evolutionary approach to ecosystem functioning

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The more diversified in habits and structure the descendants of our carnivorous animal became, the more places they would be enabled to occupy. What applies to one animal will apply throughout all time to all animals. . . So it will be with plants. It has been experimentally proved, that if a plot of ground be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised. The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground. Hence, if any one species of grass were to go on varying, and those varieties were continually selected which differed from each other in at all of the same manner as distinct species and genera of grasses differ from each other, a greater number of individual plants of this species of grass, including its descendants, would succeed in living on the same piece of ground.

Charles Darwin (1859) (1)

Darwin bolstered his case for evolution by natural selection by noting a link between diversification and abundance, and even between what we would now call plant diversity and ecosystem productivity (2). Although Darwin had a seamless view of evolutionary, population, and ecosystem processes, by the 1980s these had become the domains of disparate disciplines. This is changing, at least in part because of recent work demonstrating that Darwin was, indeed, correct: a greater number of terrestrial plant species can lead to greater ecosystem productivity and resource use (3–6) (Fig. 1). Additional work has shown that greater diversity can lead to greater ecosystem predictability and temporal stability (7–9). Such results have reopened long-dormant questions concerning why and how diversity might affect population, community, and ecosystem processes. The pursuit of these questions is leading to a new synthesis of evolutionary and ecological mechanisms, as illustrated in the work of Norberg and colleagues (10) in this issue of PNAS. Their work extends a growing body of theory linking species traits and spe-



**Fig. 1.** Recent experimental studies of the effects of the number of plant species on ecosystem productivity (3–6) have supported Darwin's assertion that greater diversity leads to greater productivity. Shown is the Cedar Creek biodiversity experiment, located in east-central Minnesota (5).

cies diversity to ecosystem functioning (11–15).

The theory of Norberg and colleagues (10) is an advance on at least two fronts. First, their model explicitly links evolutionary dynamics to ecosystem functioning. Earlier models did not consider evolutionary change and assumed that species had discrete, fixed traits. To a great extent, this was deliberate. The earlier models were designed to predict the "pure" effects of diversity by randomizing and averaging across confounding factors, especially differences in species composition. In particular, to determine the effect of species number (diversity) on ecosystem functioning in these models, species compositions were determined by many separate random draws of various numbers of species from a common species pool. In essence, in these models greater diversity led to a better match between a fixed, unchanging pattern of habitat environmental heterogeneity and the traits of the competing species, and thus to more complete use of limiting resources and greater productivity. This approach allows the theoretical determination of the pure effects of diversity because it uses unbiased (random) species compositions. However, by so doing, this approach implicitly assumes that community compositions are determined simply by random assembly. Moreover, the traits of organisms cannot evolve in response to environmental changes.

Nature is rarely as simple or pure as the idealized cases that are constructed in the pursuit of scientific insight. Instead of assuming that all potential combinations of species were equally likely to occur, Norberg *et al.* modeled ecosystems as complex adaptive systems. In their nonequilibrium model, there was no optimal match between organismal traits and environmental conditions because the environment was constantly changing, favoring different traits at different times. Rather, the temporal dynamics of the environment and its effects on interactions among organisms with different heritable traits determined which traits persisted and their abundances. The end result of these evolutionary dynamics was that or-

ganismal traits tracked environmental change, albeit with a time lag.

Much as suggested by Darwin, Norberg and colleagues show that such evolutionary dynamics lead to greater productivity than would have been possible even with the best possible fixed, nonevolving single most-productive phenotype. This important contribution demonstrates, for self-assembled, evolving communities, that greater diversity leads to greater long-term productivity precisely because greater phenotypic diversity increases the quality of the match between organismal traits and fluctuating habitat conditions. This provides an interesting variation on existing "sampling effect" models (11–16). Here, the sampling pattern, by changing through time, allows persistence of a suite of traits, rather than a single trait. Although sampling effects have been dismissed by some authors (16, 17) as artifacts, the work of Norberg *et al.* demonstrates a clear link between environmental fluctuations, persistence of trait diversity, and ecosystem functioning.

As one might expect, models that include interactions among organisms with different phenotypes can be complex. The model of Norberg *et al.* is so complex that its whole-community properties, such as the dependence of productivity on phenotypic diversity, can be determined only via numerical solution. However, Norberg *et al.* develop a simple, analytically tractable version of their model by extending the moment closure approach developed for population genetics by Barton and Turelli (18). This model and its insights are the

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second major advance of Norberg *et al.*'s paper.

Instead of explicitly modeling the dynamics of individuals of each phenotype, the simplified model approximates this by using the distribution of phenotypic traits (the mean and its variance) and the effects of this distribution of traits on the dynamics of whole-system biomass. Although higher moments are ignored, the simplified model provides a good fit to simulations of the full model. The first differential equation of the simplified model (equation 8 in ref. 10) links the rate of change of total biomass to the mean phenotypic trait and phenotypic variance. In this equation, increased phenotypic variance, which is a direct measure of greater diversity, can lead to decreased productivity because higher phenotypic variance means that there are more individuals with a trait other than the current optimum. Their second differential equation (equation 9 in ref. 10), which is closely related to the fundamental theorem of natural selection, describes how the mean phenotypic trait changes. This equation shows that the rate at which traits can track environmental change is greater when there is greater phenotypic variance. The net effect of these two dynamic processes is that greater phenotypic variance can lead to greater whole-system productivity for a community composed of individuals evolving in response to environmental change. This demonstrates, for a case never before explored, the same sort of diversity effect observed in simpler, earlier theory.

The work of Norberg and colleagues suggests several new avenues for exploring the effects of diversity on ecosystem processes, including measuring diversity via the variance in organismal traits and having communities assemble and change by adaptive processes. It also raises new questions. For instance, within the framework of their model, how does the total biomass produced during an average environmental cycle depend on phenotypic variance, mean growth rate, and the rate of environmental change? Also, earlier theory measured diversity as the number of species in a community whereas Norberg *et al.* used the variance in phenotypic traits. Might a hybrid definition provide even deeper insight? If, as seems likely, the range of phenotypic variance within each species is small compared with the total phenotypic variance that is maintained in a community or that maximizes an ecosystem process (and it is not yet clear if or when these are one and the same), there might be joint effects of species number and total-community phenotypic variance on ecosystem processes. For instance, increases in species number could increase ecosystem functioning by filling in empty regions of the phenotype distribution even though this did not change total-community phenotypic variance.

In total, the work of Norberg and colleagues is an important step in the development of more realistic, yet general, models linking diversity and ecosystem functioning. Perhaps most importantly, this and other work exploring the mechanisms underlying effects of diversity on ecosystem functioning are bringing us closer to a new synthesis of evolutionary, population, and ecosystem perspectives and to a more seamless vision of the natural world.

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