Causes, consequences and ethics of biodiversity

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The existence of so great a diversity of species on Earth remains a mystery, the solution to which may also explain why and how biodiversity influences the functioning of ecosystems. The answer may lie in quantifying the trade-offs that organisms face in dealing with the constraints of their environment. Societal responses to the loss of biodiversity also involve trade-offs, and the elaboration of these will be essential in developing wiser environmental ethics and policy.

The most striking feature of Earth is the existence of life, and the most striking feature of life is its diversity. This biological diversity, or biodiversity, has long been a source of wonderment and scientific curiosity, but is increasingly a source of concern. Human domination of Earth's ecosystems[1] is markedly reducing the diversity of species within many habitats worldwide, and is accelerating extinction. One of the more pragmatic questions raised by these threats to biodiversity is the extent to which this loss of biodiversity matters; that is, are stability, productivity and other aspects of the functioning of both managed and natural ecosystems dependent on biodiversity?

There are strong reasons to hypothesize, as did Darwin[2] and Elton[3], that biodiversity might impact ecosystem processes. But ecology is no longer a discipline in which natural history observations and simple verbal logic hold sway. The rekindled interest in the potential effects of biodiversity on ecosystem processes, which followed the publication in 1993 of a book edited by Schulze and Mooney[4], is occurring in a discipline for which hypotheses are now tested against the results of field experiments, mechanistic theory and quantitative field observations. Anything less than the concordance of all three lines of evidence leads to the modification or rejection of hypotheses. Given that this topic became a principal focus of scientific inquiry only about seven years ago, it is not surprising that it remains contentious. Indeed, the greatest surprise may be the rapidity, breadth and depth of work that already has occurred, and the generalities that are emerging from it.

Five papers in this issue summarize this work. Purvis and Hector (pages 212–219), McCann (pages 228–233), and Chapin and collaborators (pages 234–242) review and synthesize recent experimental, theoretical and observational studies that have demonstrated links between biodiversity and the stability, productivity and nutrient dynamics of ecosystems. Gaston (pages 220–227) summarizes global patterns of biodiversity and some possible explanations for these patterns. Margules and Pressey (pages 243–253) discuss strategies for the preservation of biodiversity.

The effects of biodiversity on ecosystems

In broad summary, these reviews show that, on average, greater diversity leads to greater productivity in plant communities, greater nutrient retention in ecosystems and greater ecosystem stability. For instance, grassland field experiments both in North America (Fig. 1)[5,6] and across eight different European sites, ranging from Greece in the south and east to Portugal and Ireland in the west and Sweden in the north[7], have shown that each halving of the number of plant species within a plot leads to a 10–20% loss of productivity. An average plot containing one plant species is less than half as productive as an average plot containing 24–32 species[5–7]. Lower plant diversity also leads to greater rates of loss of limiting soil nutrients through leaching, which ultimately should decrease soil fertility, further lowering plant productivity.

Both laboratory and field studies have shown that ecosystem processes are more variable (less stable or reliable) at lower diversity (see review by McCann, pages 228–233, and refs 8–10). The greater stability of more diverse ecosystems seems to result from three processes[11–14]. The first is comparable to the economic process that causes a more diverse investment portfolio to be less volatile. Because species, like corporations, differ from each other, they tend to respond somewhat independently to environmental variability. The more species that such variability is averaged across, the less variable is their total[11]. Second, species within a given trophic level often compete with each other, which causes their abundances to negatively covary. When one species declines, another is freed from competition and increases. This negative covariance reduces the variability of the community as a whole[13,14]. Finally, measures of temporal stability compute variability relative to mean abundance, such as by using the ratio of community abundance to its temporal standard deviation. The tendency for community

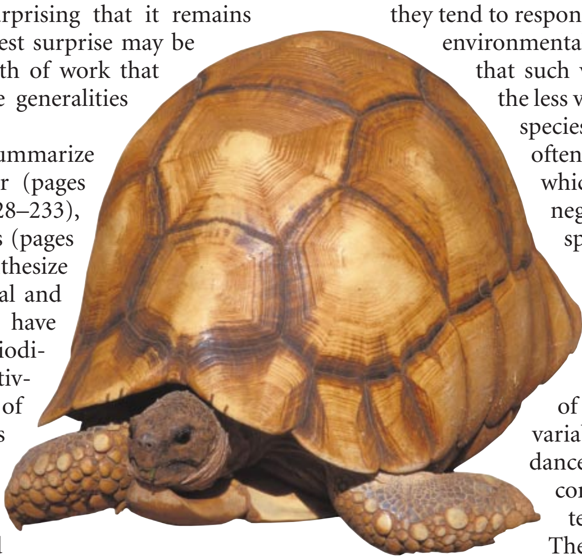

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Figure 1 Biodiversity experiments, such as this one in Minnesota[6] or the other experiments reviewed by Chapin *et al.* (pages 234–242) and by Purvis and Hector (pages 212–219), have shown that a greater number of plant species leads to greater community productivity. In the experiment shown, 245 plots, each 9 m × 9 m, were assigned randomly to have from 1 to 16 prairie plant species, with the species composition of each plot being separately chosen at random[6]. Species composition and plant diversity were both strong determinants of ecosystem functioning.

abundance to increase as diversity increases thus causes this ratio, which is a measure of stability, to increase as diversity increases[14].

In total, biodiversity, which ten years ago was considered unimportant by most ecosystem ecologists, has now been shown to impact significantly upon many aspects of ecosystem functioning. Diversity must now be added to the list of factors — including species composition, disturbance regime, soil type and climate — that influence ecosystem functioning. The recent rediscovery of the importance of biodiversity highlights an under-appreciated truth — although society is dependent on natural and managed ecosystems for goods and services that are essential for human survival, we know all too little about how ecosystems work.

Two sets of unanswered scientific questions come to the forefront. First, why is the world so diverse; that is, what forces and processes led to the evolution and persistence of so many species? This is not merely an academic question. The processes that allow interacting species to coexist in an ecosystem simultaneously influence the productivity, nutrient dynamics and stability of that ecosystem. Second, what are the mechanisms by which the loss of diversity impacts the functioning of ecosystems, how general are these mechanisms, and how important is biodiversity relative to other factors that influence ecosystem functioning? In addition, the realization that human actions are harming, perhaps irreversibly, the ecosystems upon which humans depend raises a third, philosophical question: what should be the role of scientists and science in the development of ethics and policy?

Coexistence and ecosystem functioning

Both our understanding of the effects of biodiversity on ecosystem processes, and the effectiveness of alternative strategies for the preservation of biodiversity, are limited by our knowledge of the mechanisms that maintain diversity. The mechanisms most relevant to ecosystem functioning are those that maintain diversity on the local scales within which individuals of one species interact with individuals of other species. It is from such interactions among individuals of different species that diversity is expected to impact ecosystem processes.

What are these mechanisms of coexistence? At present there are an abundance of alternative hypotheses but no clear demonstrations of the actual processes that maintain the diversity of species-rich ecosystems. In a general sense, coexistence requires the existence of evolutionarily persistent interspecific trade-offs in the abilities of species to deal with the factors that constrain their fitness and abundance. However, there are many potential constraints and trade-offs. Species may coexist because of interspecific trade-offs (1) between their competitive abilities and their dispersal abilities; (2) between their competitive abilities and their susceptibility to disease, herbivory or predation; (3) between their abilities to live off average conditions and their abilities to exploit resource pulses; or (4) between their abilities to compete for alternative resources in a heterogeneous landscape[15–18].

The effects on ecosystem functioning of many such mechanisms of coexistence have yet to be determined theoretically. However, it is already clear that the underlying mechanisms of coexistence can greatly influence how diversity affects ecosystem processes[19,20]. Consider, for instance, plant species that coexist in a spatially heterogeneous habitat because of differences in both the soil pH and the temperature (which varies seasonally) at which each grows optimally (Fig. 2a). Such niche differentiation[20] causes the predicted productivity of plant communities to be an increasing function of plant diversity (Fig. 2b). Moreover, the pattern of this increase is such that there are some species combinations at a given level of diversity that are more productive than any possible combination of fewer species (Fig. 2b). The greater productivity of higher diversity communities occurs because, in such heterogeneous habitats, each species is a superior performer in only a portion of sites. Clearly, the magnitude

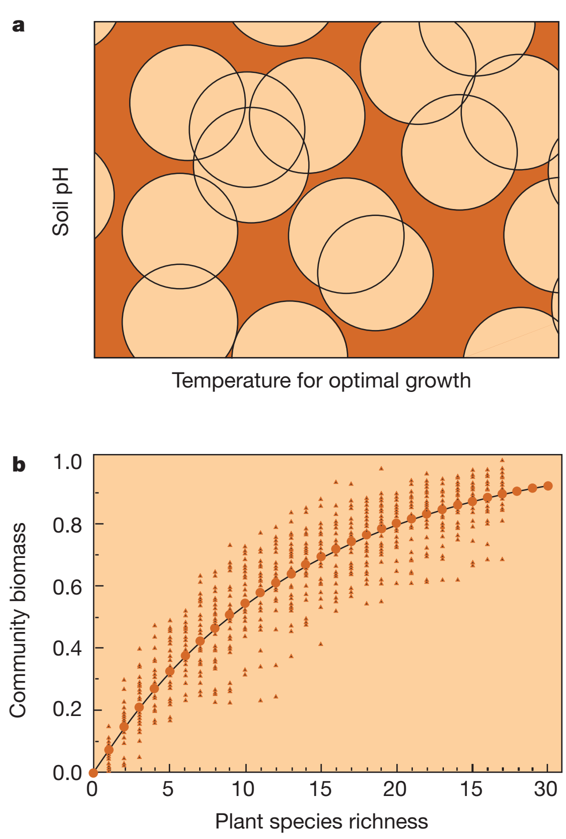

Figure 2 Niche differentiation and productivity. **a**, A simple model — the 'snowballs on the barn' model — of niche differentiation and coexistence[20]. The range of conditions in which each species can exist is shown with a circle, the position of which is defined by its centre. By randomly choosing locations for various numbers of circles (species), it is possible to calculate the effect of diversity on the 'coverage' of the heterogeneous habitat. The amount of such coverage is proportional to community biomass. **b**, Results of simulations (triangles) and of an analytical solution (solid curve) to the effects of diversity on community productivity for the snowballs on the barn model[20].

of this effect increases as heterogeneity or diversity increase. Increased diversity leads, on average, to increased 'coverage' of the habitat conditions, that is, to increased efficiency of resource capture and use, because diversity increases the chance that the species that are better able to handle particular conditions are present. Assuming that species are chosen at random, diversity is a simple way to measure the range and coverage of species traits in a community.

In contrast, consider a case in which interspecific interactions are based on direct antagonism and not on efficiency of resource use. For a simple formulation, let there be an interspecific trade-off between competitive ability and productivity. Species that achieve greater productivity in monoculture would be poorer competitors, attaining lower abundances when competing. Because greater diversity increases the chance that a competitively superior but lower-yielding species would be present, productivity would, on average, be a decreasing function of diversity. This is a simple variant on the sampling-effect model[20–22], here modified to have better competitors be less, rather than more, productive.

What, then, is implied by available experimental results, which have shown that productivity is an increasing function of plant species diversity? They indicate that coexistence through niche differentiation and related processes may be more prevalent in nature than coexistence through antagonism and related processes, at least for the types of communities studied so far. Expressed another way, much of nature may have a free-market economy, structured by the efficiencies of open competition among species, rather than an economy structured by pre-emption and other monopolistic practices. Such speculations may be premature, especially because complex systems containing many trophic levels (for example, plants, decomposers, herbivores and predators) are, as yet, poorly studied. However, they highlight the conceptual links between economics and ecology — disciplinary links that must be strengthened if ecological knowledge is to be used to help create a sustainable human economy.

Societal trade-offs and ethics

The progress made during the past seven years in understanding these issues underscores the potential implications of habitat simplification and loss of diversity for the ecosystem goods and services[23] upon which humans depend. The species presently inhabiting Earth are the result of over 3 billion years of natural selection that likely favoured efficiency, productivity and specialization. These organisms are the catalysts that capture and transform energy and materials, producing, among other things, food, fuel, fibre and medicines. These species recycle wastes, create pure drinking water, drive global biogeochemical cycles that created and maintain an aerobic atmosphere, regulate global climate through effects on greenhouse gases and local climate through effects on evapotranspiration, generate soil fertility, and provide other ecosystem goods and services[23]. In addition, the Earth's biodiversity is the source of all crops and all pollinators of crops, of all livestock, and of many pharmaceuticals and pesticides. Just three crops — corn, rice and wheat — provide about 60% of the human food supply. The viability of these crops depends on the maintenance of high genetic diversity[24], which can allow, among other things, development of strains that are resistant to emerging and evolving diseases and pests[25]. In the long term, food stability will require development of new crops from what are now wild plants, because disease or pesticide-resistant pests will cause the loss of current crops, just as disease caused the loss of chestnut, elm and other tree species from North American forests.

Humans, like all other organisms, experience trade-offs. The loss of biodiversity will diminish the capacity of ecosystems to provide society with a stable and sustainable supply of essential goods and services, but many of the very actions that harm biodiversity simultaneously provide valuable societal benefits. There exists a trade-off defining the net benefits that society receives from the various ways that humans could use and impact nature, but, as yet, this is poorly defined. This trade-off itself is likely to shift through time in response to the remaining amounts and states of various resources, including biodiversity. The amounts and states of biotic resources have changed rapidly during the past century, as global population increased 3.7-fold and per capita gross domestic product, a reasonable proxy for consumption, increased 4.6-fold[26]. It seems likely that environmental policy that is optimal from a societal perspective would be markedly different now from that of 250 years ago. However, we still use environmental and land-use ethics, codified in law, that were articulated during the era when the human population, at one-tenth its present size, tamed wilderness with axe and ox.

Science has much to contribute to dialogues on policy and ethics. Although academic institutions seem to value such contributions less than contributions to peer-reviewed journals, this is short-sighted. Ultimately, society invests in science because advances in scientific knowledge benefit society. The ethics of science cannot eschew involvement in public discourse. Science must contribute, in an open, unbiased manner, to relevant issues.

Because of the emergence of human domination of global ecosystems, society faces new, tough trade-offs. These include trade-offs between the current benefits and the future costs of environmental damage, and between benefits to a few and costs to many. Research is needed to quantify these trade-offs, and the work done so far on biodiversity provides a good start. Additional work, at the interface between ecology and economics, is needed to quantify the immediate and long-term costs and benefits of alternative actions.

The world that will exist in 100 and 1,000 years will, unavoidably, be of human design, whether deliberate or haphazard. The principles that should guide this design must be based on science, much of it done only sketchily to date, and on ethics. Ethics should, among other things, apportion costs and benefits between individuals and society as a whole, and between current generations and all future generations. A sustainable world will require an ethic that is ultimately as incorporated into culture and as long lasting as a constitutional bill of rights or as religious commandments. The Earth will retain its most striking feature, its biodiversity, only if humans have the prescience to do so. This will occur, it seems, only if we realize the extent to which we use biodiversity. □

1. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human domination of earth's ecosystems. *Science* **277,** 494–499 (1997).
2. Darwin, C. *The Origin of Species by Means of Natural Selection* (reprinted by The Modern Library, Random House, New York, 1859).
3. Elton, C. S. *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).
4. Schulze, E. D. & Mooney, H. A. *Biodiversity and Ecosystem Function* (Springer, Berlin, 1993).
5. Tilman, D., Wedin, D. & Knops, J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379,** 718–720 (1996).
6. Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. The influence of functional diversity and composition on ecosystem processes. *Science* **277,** 1300–1302 (1997).
7. Hector, A. *et al.* Plant diversity and productivity experiments in European grasslands. *Science* **286,** 1123–1127 (1999).
8. Tilman, D. & Downing, J.A. Biodiversity and stability in grasslands. *Nature* **367,** 363–365 (1994).
9. McGrady-Steed, J., Harris, P. M. & Morin, P. J. Biodiversity regulates ecosystem predictability. *Nature* **390,** 162–165 (1997).
10. Naeem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390,** 507–509 (1997).
11. Doak, D. F. *et al.* The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.* **151,** 264–276 (1998).
12. Tilman, D., Lehman, C. L. & Bristow, C. E. Diversity-stability relationships: statistical inevitability or ecological consequence? *Am. Nat.* **151,** 277–282 (1998).
13. Tilman, D. Biodiversity: population versus ecosystem stability. *Ecology* **77,** 350–363 (1996).
14. Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80,** 1455–1474 (1999).
15. Hastings, A. Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.* **18,** 363–373 (1980).
16. Armstrong, R. A. & McGehee, R. Competitive exclusion. *Am. Nat.* **115,** 151–170 (1980).
17. Huisman, J. & Weissing, F. J. Biodiversity of phytoplankton by species oscillations and chaos. *Nature* **402,** 407–410 (1999).
18. Tilman, D. *Resource Competition and Community Structure* (Monographs in Population Biology, Princeton Univ. Press, 1982).
19. Loreau, M. Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl Acad. Sci. USA* **95,** 5632–5636 (1998).
20. Tilman, D., Lehman, C. L. & Thomson, K. T. Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl Acad. Sci. USA* **94,** 1857–1861 (1997).
21. Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110,** 449–460 (1997).
22. Aarssen, L. W. High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* **80,** 183–184 (1997).
23. Daily, G. C. *Nature's Services: Societal Dependence on Natural Ecosystems* (Island, Washington DC, 1997).
24. Fehr, W. H. *Genetic Contributions to Yield Gains of Five Major Crop Plants* (Crop Science Society of America, Madison, WI, 1984).
25. Roelfs, A. P. Genetic control of phenotypes in wheat stem rust. *Annu. Rev. Phytopathol.* **26,** 351–367 (1988).
26. Maddison, A. *Monitoring the World Economy 1820-1992* (Development Centre of the Organization for Economic Co-operation and Development, Paris, 1995).