



Impacts of Biodiversity Loss

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Science **336**, 552 (2012);
DOI: 10.1126/science.1222102

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resolved in places where large recent changes have occurred (9), providing a basis for process understanding that can be extrapolated to regions that are still stable.

Guidance for integrating the new glaciological models with existing research can be gained from the experience of the Intergovernmental Panel on Climate Change and related efforts to assess likely ocean-atmosphere change. The results presented to policy-makers with greatest confidence are those that are derived from fundamental physics, are seen in a hierarchy of models for physically similar reasons, and have been successfully “retrodicted” in paleoclimatic and instrumental records; failure of any of these reduces confidence.

A coordinated modeling effort is essential to gain the understanding and achieve the successful retrodiction that increase confidence in projections. However, a measure of heterogeneity in such activity is just as important. The mean behavior of ~20 general circulation models matches observed climate data much better than any single model (10), providing reason to doubt the apparent efficiency of moving forward with one model.

The improvement provided by full-stress models comes at a large computational cost, leaving much room for nimble but simplified models. For example, the need to test against paleoclimatic archives, together with the >100,000-year time scales of central ice-sheet regions, cannot be met with the full-resolution versions of the most complex models. Also, performance of simpler models is easier to test in situations with analytic solutions. During assimilation and forward

modeling, uncertainties in a host of parameters can affect outcomes; “massive ensemble” analyses (11), which show whether particular solutions are excluded, allowed, or likely, are almost entirely the realm of simplified models. Comprehensive model runs can be viewed as numerical experiments; efforts to understand the outcomes of such experiments at a more fundamental level can provide important insights to the climate system (12, 13). Thus, the advent of the comprehensive modeling tools is likely to increase the need for simpler models.

Complex modeling is far from the only challenge on the road to useful ice-sheet projections. Model results and data both show that ice sheets can exhibit threshold behavior (14), which may depend on small features that are not well sampled by available data sets. Maintenance of observational capacity, from ice cores to satellites, will be crucial to ensure that current and future ice-flow and ice-thickness changes are measured. The lack of a firm understanding of ice-sheet–ocean interaction, constrained by reliable ocean data, remains a critical obstacle to understanding future changes.

Still, there is cause for optimism. With the ability to determine thickness, speed, elevation change, and other characteristics of the ice sheets from space and aircraft, to survey them from the surface, to plumb their depths with cores, and to model them with a hierarchy of approaches, including full-stress models coupled to global climate models, today looks like the start of a new phase of glaciological research. Until rigorous model-based sea-level projections can be brought to frui-

tion, however, guidance is likely to continue to rely on semi-empirical approaches (1), analogy to paleoclimatic situations, physically limiting estimates, expert elicitations, and results of simpler models.

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Acknowledgments: Partial funding was provided to R.B.A. through grants NSF 0424589, 0909335, ANT-0944286, and NASA NNX-10-AI04G, and to I.J. through grants NASA NNX-11AC23G and NSF ANT-0852697.

10.1126/science.1220530

ECOLOGY

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Historically, ecologists and evolutionary biologists have treated the variety of life on Earth as if it were a simple by-product of the physical and chemical variation that generates biological diversity and allows it to persist. However, this perspective changed in the 1990s, when scientists began to manipulate biodiversity in controlled environments and found that it can act as an independent variable that directly controls

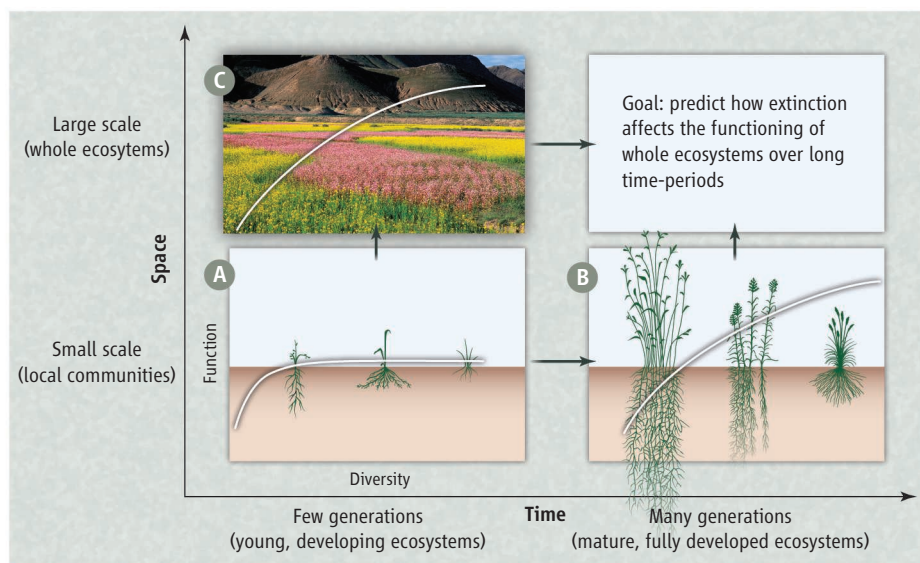
ecosystem-level functions, such as nutrient cycling and biomass production (1–4). The idea that biodiversity might control—rather than just respond to—Earth’s biophysical processes was foreign to many researchers (5). But by 2010, more than 600 manipulative experiments had been performed, spanning much of the tree of life and most major biomes on the planet (6). We now know that biodiversity regulates many ecosystem-level processes, including some that are essential for providing goods and services to humanity (6–9). On page 589 of this issue, Reich *et al.* (10) provide important novel insights into

How much diversity is needed to maintain the productivity of ecosystems?

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The authors reanalyze data from two classic biodiversity studies that have been running for more than a decade at the Cedar Creek Ecosystem Science Reserve in Minnesota. By fitting data collected over a 15-year period to several mathematical functions (linear, log, power, and hyperbolic), the authors quantify the form of the relationship that describes how plant species richness influences the production of plant biomass. They show that the effects of biodiversity on productivity change from saturating functions that are prominent

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Scaling diversity-function relationships. Since 1990, more than 600 experiments have manipulated the diversity of plants, animals, fungi, protozoa, and bacteria in a variety of Earth's biomes. These studies have shown that ecosystem functions like nutrient cycling and biomass production are positively related to biodiversity, but that relationships saturate at relatively low levels of diversity (A). Reich *et al.* have reanalyzed results from two long-term studies of grassland plants and found that although saturating functions are prominent early in the studies, diversity-function relationships ultimately become monotonically increasing given enough time (B). Short-term experiments may thus underestimate the number of species needed to maintain ecosystem-level processes. If the results prove to be general, Reich *et al.* will have quantified how the ecological impacts of extinction scale through time (A to B). If others can similarly quantify how diversity-function relationships change with the spatial extent of studies (A to C), we would have scaling relationships to estimate the fraction of species needed to maintain ecological processes in more realistic ecosystems (D).

early in the experiments (see the figure, panel A), to monotonically increasing functions later in the experiments (panel B).

Reich *et al.* argue that the reason for this change is that it takes time for species to express the biological traits that allow them to fill their various ecological niches. They present a set of calculations that estimate how much of the diversity effect in any given year is driven by processes involving two or more species (called complementarity). They show that complementarity grows stronger through time, and this trend is associated with a greater divergence in the biological traits of species in the experimental plots. These trends are not conclusive evidence that niche differences are the underlying cause of the reported patterns, but they hint at the possibility that biological "niche space" becomes more completely filled as communities interact and assemble through time.

Several studies have shown that diversity effects grow stronger with time (11, 12), but Reich *et al.* go further by quantifying how the shape of the diversity-function relationship—which tells us what fraction of species is required to maintain ecosystem functions—changes through time. If biodiversity has a saturating effect on ecosystem processes, as most prior studies suggest, this implies that

some fraction of species are functionally "redundant," and can be lost with little or no impact on ecosystem processes. Ehrlich and Ehrlich (13) compared biological redundancy to the redundancy of rivets on an airplane wing. Loss of one or few rivets will not affect the performance of the plane, because wings are engineered with an excess of rivets. But lose one too many rivets, and the loss could have catastrophic consequences for passengers on the plane.

If, however, the relationship between biodiversity and ecosystem functioning is monotonically increasing, as Reich *et al.*'s reanalyses suggest, then each extinction would produce an incremental decrease in the functioning of ecosystems. This scenario would be far more pressing for conservation. A notable fraction of Earth's biodiversity has already been lost, and given current rates of extinction, much more is likely to be lost in the coming century (14). If the results of Reich *et al.* hold generally true, then biodiversity loss has probably already begun to degrade essential processes that sustain the productivity of ecosystems.

Reich *et al.*'s findings emphasize the importance of long-term studies, such as those sponsored by the U.S. National Science Foundation's Long Term Ecological Research

Program that partially funded the Cedar Creek experiments. Most natural communities do not develop on the 1- to 3-year time frame of a typical grant, which is the scale of the average experiment. It is, therefore, possible that many biodiversity experiments to date have revealed just the tip of the iceberg—the short-term, transient effects of biodiversity on ecosystem processes. The real impacts of diversity loss could be much greater.

It remains to be shown whether the results of Reich *et al.*'s study are general, or whether something unique about the species pool, environmental conditions, or experimental methodologies make the experiments at Cedar Creek the exception rather than the rule. Resolving this will require comparison to other long-term studies, and reanalysis of data from biodiversity experiments involving even longer population dynamics than those at Cedar Creek (such as studies performed with model systems of bacteria or algae).

But if the conclusions of Reich *et al.* hold generally true, and monotonically increasing diversity-function relationships are indeed the norm, then this study moves us an important step closer to predicting the ecological consequences of diversity loss in real ecosystems, where life forms have evolved and interacted for many generations (see the figure, panel B). The study should also stimulate others to ask similar questions about how the form of diversity-function relationships changes with the spatial scale of experiments (see the figure, panel C). Once we know how diversity-function relationships scale in both time and space, we will have the statistical models needed to forecast the ecological consequences of extinction from whole ecosystems. For a field of research that did not even exist until the 1990s, development of such models would represent monumental progress in a remarkably short time.

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