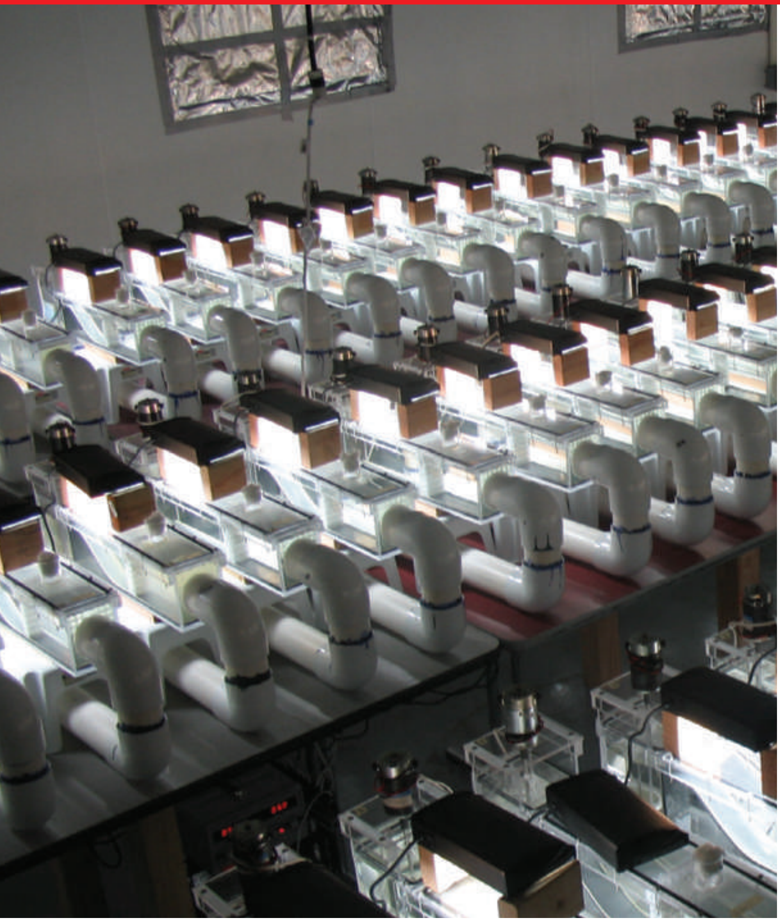

B. CARDINALE

RACK AND FIELD

Ecologists have struggled to reconcile what they see in the lab and in the wild. But both views are needed to understand the effects of extinction, finds **Virginia Gewin**.

More than 100 streams run through Bradley Cardinale's laboratory. Some trickle, others gush. Some are home to one species of freshwater algae, others to eight. And they were all created to answer a simple ecological question.

Cardinale wants to know how the number of species living in a stream affects the quality of water that flows through it. The problem calls for controlled, replicable experiments, hence the artificial streams in his lab at the University of California, Santa Barbara. But he must also show that the results he sees in the lab apply to the water found in natural streams. So he is running a parallel experiment in the Sierra Nevada mountain range to compare how communities with naturally low and high species diversity clean up the streams that flow there (pictured above).

Tackling this question has taken Cardinale five years, in part because he has gone to great pains to include an aspect of reality in his lab experiment — water flow, which influences diversity. In the next stage he will have to quadruple the number of streams to analyse the effects of adding one algae-eater and its predator into the system. "The complexity of this work is invigorating and, at times, frustrating," Cardinale says. "But in an era when up to half the world's species hang in the balance, we must confront the complexity head on."

> "The complexity of this work is invigorating and, at times, frustrating."
> — Bradley Cardinale

Within that complexity, hope Cardinale and others, lie answers to the question of whether the current wave of extinctions will just result in fewer pretty flowers and birds to look at, or whether it will mean poorer soils, more carbon in the atmosphere and the loss of billions of dollars' worth of 'ecosystem services' — natural processes that benefit humans, such as water purification, pollination and pest control. How to measure the impact of species loss on ecosystems and their services has been the subject of lengthy, inconclusive and sometimes bitter debate among ecologists. It has taken a long time to work out the best way to ask the question, with lab and field experiments often pitted against one another, and researchers agonizing over whether they should sacrifice biological reality for experimental purity.

In recent years, ecologists such as Cardinale have realized that 'field with lab' is a more productive path than 'field versus lab'. Findings from such combined studies suggest that researchers have underestimated how important biodiversity is to ecosystem functioning, which is both vindicating and sobering to those who stress nature's practical value. The next step, they say, is to try to use this hard-won knowledge to guide efforts to save what's left, and to help restore natural places to make them useful to human needs. "We need to amass the science necessary to make predictions now, before more species go extinct," says Cardinale, "so that we can understand how many species must be restored to degraded ecosystems in order to regain functions like pest or disease control."

Variety: the spice of life

By the mid-1990s, most of the world seemed to believe that conserving the species in an ecosystem was important to maintaining its natural functions. In December 1993, countries that are party to the United Nations Convention on Biological Diversity committed to developing strategies to conserve and sustainably use biological diversity because, the convention argued, conservation would provide environmental and economic returns. Yet up until then, there had been little direct evidence of diversity's importance for environmental and human welfare. The debate swung backwards and forwards for decades, between ecologists' intuition that diverse ecosystems must be healthier than impoverished ones, and theoretical studies that suggested that as the number of species in a system grew, more extinctions would be expected[1]. With the convention, governments, along with the researchers they look to for guidance, had an urgent need to clarify the relationship between diversity and function, so that they would know what was important to conserve.

In 1994, two papers brought new experimental approaches to the question. Using a long-term study of grassland plots in Minnesota[2], ecologists David Tilman of the University of Minnesota in St Paul and John Downing, who was then at the University of Montreal, Canada, found that plots with more species were less affected by droughts, showing smaller reductions in biomass, and recovering to their pre-drought state more quickly. In the same year, Shahid Naeem and his colleagues at Imperial College London used the 'Ecotron' — a system of walk-in cells containing square-metre plots, each stocked with differing numbers of plant, herbivore, decomposer and predator species — to show that more diverse microcosms produced more biomass and consumed more carbon dioxide. A doubling or tripling of the number of species resulted in a roughly equivalent rise in productivity[3].

Tilman and Downing saw their results as support for the idea that the more species you have, the more likely a system will stay productive in the face of a drought or other crisis, because some species will be tolerant to the stress. Naeem's team suggested that the key lay in division of labour: a more diverse community is more fully able to exploit the spectrum of resources, such as light, soil nutrients or water availability. Either way, the implications for conservation were enormous. "If the number of species was important, then we had a responsibility to conserve every species," says Cardinale.

But many ecologists challenged the papers' conclusions. Until then, most scientists had believed that an ecosystem's function depended on whether it contained key species, with the total number of species having at most a minor effect. One of the fiercest critics, Michael Huston of Texas State University in San Marcos, thinks that the 1994 studies failed to exclude this possibility. "These experiments were designed, intentionally or not, to always show that more species have a higher level of ecosystem function," he says.

Huston argues that any relationship between diversity and function in those studies was probably due to a 'sampling effect'[4]; that is, higher productivity in diverse ecosystems could be explained by the greater probability that they would contain one or two highly productive species doing all the ecological heavy lifting. "No one disagrees that biodiversity influences ecosystem function," Huston says, "but is it the number of species or the properties of specific species?" Conservation efforts, he argues, shouldn't be based on the understanding that more species make for better ecosystem functions.

> **"These experiments were designed, intentionally or not, to always show that more species have a higher level of ecosystem function."**
> — Michael Huston

Some charged the researchers with blatant bias, accusing them of interpreting their studies so as to advance a political agenda for conservation by showing that biodiversity was economically valuable and important to human well-being. "Those comments were said in private conversations, and I personally found them astounding," says Tilman. He knew from the start that the study's conclusions would cause controversy, so he sat on his data for years, testing alternative hypotheses. "I didn't quite believe the results myself at first," he says. But Naeem, a postdoc at the time, and now at Columbia University in New York, was surprised that what he calls his "innocent experiment" caused such a stir. He says that his adviser, John Lawton, a community ecologist at Imperial College London, was concerned that Naeem's experimental approach would jeopardize his nascent career. In ecology, says Naeem now, any experimental approach is liable to draw criticism. "The only thing that is real in science is what can be seen through a pair of binoculars. As soon as we start to mess with it, it becomes suspect," he says.

Even so, many ecologists spent the next decade messing with it. They built model ecosystems in an effort to control the myriad variables at work and to isolate the effects of species number. But in the quest for rigour, the experiments and the way they were manipulated became so unlike natural ecosystems that the goal — to uncover what happens when species go extinct — was sometimes missed. For example, it became customary for controlled experiments to randomize the addition or removal of species and environmental conditions, but such processes are not random in natural systems. Critics charged that ignoring the factors controlling biodiversity while studying the ecological effects of it rendered such studies irrelevant.


T. EVANS

Biodiversity in a box: 'Ecotron' chambers are used to measure effects of biodiversity on ecosystem productivity.

Heated debate

Temperatures rose as researchers took sides, some advocating the sampling effect, others arguing that efficient partitioning of resources among species was the key to increased productivity. "The debate had to happen, and it helped the community make progress to reconcile seemingly contradictory hypotheses, but it got a bit nasty," says Michel Loreau, an ecologist at McGill University in Quebec, Canada.

In 2000, Loreau and Naeem organized a meeting in Paris to encourage everyone to look at the same data and test hypotheses together. "We established a behaviour of confronting differing opinions," says Loreau. A consensus paper resulted[5], which proposed a quantitative method to parse out the effects of relationships between species versus Huston's sampling effect. It also prompted additional work to reconcile findings from theory, observation and experiment.

Most ecologists are now convinced that more-diverse ecosystems are generally more productive. To get the big picture, Cardinale led two meta-analyses, one of more than 100 experiments[6], the other of 44 (ref. 7), in which researchers had experimentally manipulated species in both artificial and natural aquatic and terrestrial systems.

The meta-analyses showed that diversity actually has a larger effect on productivity than anyone had previously documented. Mixtures of two or more species were more productive than the average monoculture 79% of the time, and mixed plots were 1.7 times more productive as those with single species[7]. The longer an experiment ran, the more pronounced the difference became, probably because ecosystem processes change as species settle into stable, complementary relationships. "We were stunned by the magnitude of diversity effects," Cardinale says. "If anything, we have underestimated the impacts of species extinction on ecosystem productivity."

The studies also revealed that although Huston's sampling effect is real, it accounts for just one-third of the overall increase in productivity. The other two-thirds is due to interactions between species and a better division of labour. A suite of different species seems to be able to partition resources in such a way that their own properties or specialties are performed more efficiently.

Like the sampling effect, however, this insight throws the spotlight back on the attributes of species. Some think that understanding how these properties, known as functional traits, contribute to ecosystem function is more useful in predicting the effects of extinctions than looking at species number. "We were so focused on the diversity of life," says Naeem, "we didn't look at the diversity of function."

J. STACHOWICZ

R. BEST

Rock and a hard place: seaweed studies compare the impacts of biodiversity in real tidal flats and artificial ones.

Bridging the gap

Many ecologists, including Tilman and David Wardle, an ecologist at the Swedish University of Agricultural Sciences in Umeå, have been pursuing this approach all along. In 2005, for example, Wardle removed specific shrub species as well as specific functional traits, such as large roots, from 30 small islands in Swedish lakes. Some islands were affected very little and some a lot, showing how site-specific a trait's effects can be[8]. "Rather than simplify the system, we started with real ecosystems and measured what happens when different species are removed," says Wardle.

In recent years, ecologists have found other ways to bridge the gap between experimental clarity and biological reality. Experimenters have covered larger scales in space and time, and have expanded analyses across multiple levels of the food web, to include plants and animals, predators and prey. "It is possible to be rigorous and relevant at the same time," says John Stachowicz, a marine ecologist at University of California, Davis.

"It is possible to be rigorous and relevant at the same time." — John Stachowicz

Like Cardinale, Stachowicz and his colleague Matthew Bracken, a marine biologist at Northeastern University's Marine Science Center in Nahant, Massachusetts, run parallel lab and field experiments. In 2008, they compared the effect of seaweed species richness on biomass in field plots on Pacific shores and in experimental tidal beds[9]. They found that more species meant a higher rate of biomass accumulation in the field, but not in the experimental chamber. They put this difference down to the fact that the chambers lacked the variability needed to pick up the effects of the division of labour, or the arrival or departure of species. They also found that the effects of biodiversity become stronger over time in the field, and suggested that many experiments did not run for long enough to see such effects.

Bracken is opening up a third front of investigation — *in silico*. His team has combined experiments with computer simulations of 3,500 combinations of seaweed species to model a larger number of scenarios than can be covered experimentally. The researchers found that with a realistic mix of species — which in nature, is controlled in part by wave exposure — more diversity meant more nitrogen uptake, whereas randomized species mixtures showed no such effect[10]. Most recently, he modelled a more realistic food web by adding snails to the mix, and found that their preference for sea lettuce (*Ulva lactuca*), the region's dominant seaweed species, increased overall plant productivity by allowing other species to grow[11].

Every small narrowing of the gap between experiment and reality reveals new things about ecosystem dynamics. But the gap may not be shrinking fast enough to reach firm conclusions — which may present a problem for conservationists who want answers now. "We're ten years away from telling policy managers which fraction of species to conserve," Cardinale says.

Cardinale is still optimistic — in a pessimistic sort of way — about ecologists' ability to provide practical advice. When he's not tending his 100 streams in the lab, he spends much of his time working in the field, wading in stream ecosystems that are losing species owing to residential development or nutrient pollution. "For many species and ecosystems, conservation efforts may have come too late," says Cardinale. But, he says, it may be possible to restore them, or to find another way to save or replace the ecological services they provide. "If we can nail down this field, we might be able to turn back the hands of time." ■

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1. May, R. M. *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, 1973).
2. Tilman, D. & Downing, J. A. *Nature* **367,** 363–365 (1994).
3. Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H. & Woodfin, R. M. *Nature* **368,** 734–737 (1994).
4. Huston, M. A. *Oecologia* **110,** 449–460 (1997).
5. Loreau, M. *et al. Science* **294,** 804–808 (2001).
6. Cardinale, B. J. *et al. Nature* **443,** 989–992 (2006).
7. Cardinale, B. J. *et al. Proc. Natl Acad. Sci. USA* **104,** 18123–18128 (2007).
8. Wardle, D. A. & Zackrisson, O. *Nature* **435,** 806–810 (2005).
9. Stachowicz, J. J., Best, R. J., Bracken, M. E. S. & Graham, M. H. *Proc. Natl Acad. Sci. USA* **105,** 18842–18847 (2008).
10. Bracken, M. E. S., Friberg, S. E., Gonzalez-Dorantes, C. A. & Williams, S. L. *Proc. Natl Acad. Sci. USA* **105,** 924–928 (2008).
11. Altieri, A. H., Trussell, G. C., Ewanchuk, P. J., Bernatchez, G. & Bracken, M. E. S. *PLoS ONE* **4,** e5291 (2009).