

ammonia — a process that forms part of the nitrogen cycle. However, the natural nitrogen cycle has been heavily influenced by human activities, which produce highly unstable forms of nitrogen known collectively as reactive nitrogen. The deposition of reactive nitrogen from the atmosphere to forests occurs mainly as a result of agricultural fertilizer use and fossil-fuel combustion, and has increased from 15 million tonnes of human-produced reactive nitrogen per year in the 1860s to 187 million tonnes by 2005 (ref. 4). Nitrogen deposition is expected to continue to increase in many regions, and has been predicted⁵ to almost double globally by 2050.

The addition of reactive nitrogen to the atmosphere by humans affects climate, and the composition and function of terrestrial and aquatic ecosystems⁴. High levels of nitrogen deposition have many damaging effects on ecosystems, but small additions can be beneficial for otherwise nitrogen-limited ecosystems, because they increase the uptake of CO₂ from the atmosphere by photosynthesis. The effect of nitrogen deposition on carbon sequestration by soil is less clear. Most studies suggest that the net effect is between 35 and 65 kilograms of carbon sequestered per kilogram of nitrogen^{6,7}. Much of the variation can be attributed to different patterns of growth and to the availability of other resources for growth.

Although low levels of nitrogen deposition might mitigate the effects of increased atmospheric CO₂ to some degree, 53–76% of this coincidental benefit is itself estimated to be offset globally⁷. This is because nitrogen deposition can stimulate net emissions of other greenhouse gases (methane and nitrous oxide) that are products of microbial activity in the soils of many ecosystems. Thus, the relative contribution of nitrogen deposition to the strength of the terrestrial carbon sink remains uncertain.

To address this problem, near-continuous atmospheric observations have been made from towers above vegetation canopies to provide estimates of CO₂ uptake (photosynthesis) and release (respiration) from and to the atmosphere, respectively. Many of these sites have been running for more than a decade, and the data are summarized by the FLUXNET Project⁸. In combination with biological and environmental data, such information has been used by researchers to examine the effect of factors such as climate variability on carbon processes at the whole-ecosystem scale at many sites around the world.

Fleischer *et al.* used FLUXNET data from 80 sites that had sufficient information about nitrogen and carbon fluxes for their analysis. They found that, for evergreen needleleaf forests in temperate and boreal zones, maximal photosynthesis under optimal environmental conditions increased with continuous nitrogen-deposition rates up to a threshold of about 8 kg of nitrogen deposition per hectare

per year. Above this value, no further increase in photosynthesis was observed.

Forests above the threshold are therefore at an intermediate stage of nitrogen saturation — a stage at which nitrogen availability exceeds microbial and plant demands, and can result in some nitrogen leaching from the ecosystem. Prolonged availability of excessive nitrogen can lead to more leaching, decreased growth and nutrient imbalances. By contrast, the evergreen needleleaf forests that responded most strongly to nitrogen deposition are in a nitrogen-limited range, within which photosynthetic capacity increases with deposition. The observed threshold is a small fraction of the nitrogen that farmers would use annually in fertilizers.

The authors also found that boreal evergreen needleleaf forests had a slightly lower photosynthetic response overall to nitrogen deposition. For both boreal and temperate evergreen forests, this translates to roughly 25 kg of carbon sequestered per kilogram of nitrogen, less than the estimated global average^{6,7,9} of 35–65.

The results are confounded by the effects of climate on photosynthesis: the nitrogen-deposition effect may be larger or smaller than Fleischer and colleagues' findings because part of the observed response is probably a result of climate. However, there is no evidence to suggest that the contribution of nitrogen deposition is zero. Although the authors attempted to determine the thresholds for other forest types, they were limited by the availability of biological data on both carbon and nitrogen processes. More comprehensive measurements of nitrogen stocks and cycling at the global network of carbon monitoring sites are required

to separate the effects of climate and nitrogen deposition on forests.

The net emissions of all greenhouse gases — including CO₂, methane and nitrous oxide — should be considered when examining the net effects of nitrogen deposition and climate on ecosystems. A better understanding of how the connections between carbon and nitrogen in the environment could change in the future is also required. Nevertheless, Fleischer and co-workers' study lays the groundwork needed to refine estimates of the effects of climate and nitrogen deposition on the terrestrial biosphere's ability to remove carbon from the atmosphere as CO₂ emissions increase. Such refinements will be necessary to improve predictions of the effects of these emissions on ecosystems at local, regional and continental scales. ■

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COMPLEX SYSTEMS

Spatial signatures of resilience

Predicting when the dynamics of a complex system will undergo a sudden transition is difficult. New experiments show that the spatial distribution of organisms can indicate when such tipping points are near. SEE LETTER P.355

STEPHEN R. CARPENTER

The divergence of dynamics towards sharply different states occurs in complex systems in fields ranging from physics and physiology to ecology and social sciences. The thresholds for these critical transitions are often unknown until surprising shifts occur. Establishing measures of the distance to a threshold — the resilience of a system — could allow researchers to compare

the stability of different systems or even anticipate an impending transition. In a paper on page 355 of this issue, Dai *et al.*¹ present a novel resilience index and use ingenious laboratory experiments to support the theory underlying it*. Their approach is based on the spatial distribution of organisms and thereby adds, quite literally, a new dimension to attempts to predict transitions.

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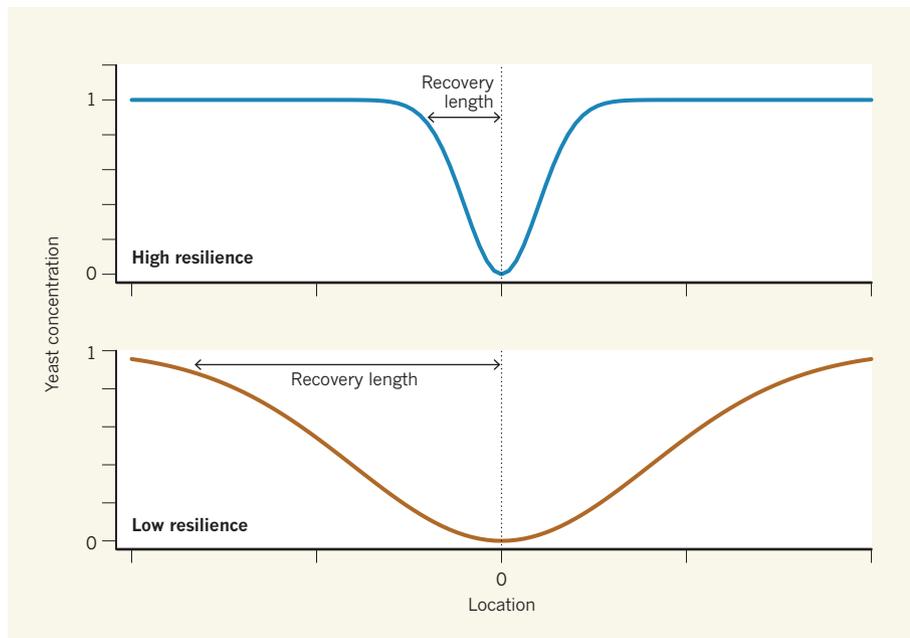


Figure 1 | Paths to recovery. Dai and colleagues¹ studied a series of linked cultures of yeast populations subject to catastrophic collapse when the dilution factor is raised above a critical threshold. They then introduced a ‘bad patch’ (position 0) in the form of a culture with a high dilution factor. Recovery length is the distance that a population must be from a bad patch for it to recover 90% of its original high concentration (a population size of 1). When the entire series of cultures was highly resilient (far from the threshold) the recovery length was short (top panel), whereas when the series of cultures had low resilience (close to the threshold) the recovery length was long (bottom panel).

Examples of the spatial distribution of organisms include the pattern of trees in a forest, of aquatic insects on the bottom of a stream, or of mussels along a rocky shoreline. In such ecosystems, a patch of unusually good habitat will be surrounded by a halo of patches with high population density, owing to the diffusion of organisms from the good patch to neighbouring sites. Likewise, a patch of poor habitat creates a halo of low population density. As the distance away from the patch of unusual habitat increases, the population density will gradually return to the average for the landscape as a whole. The distance required for the population density to return to the average value is referred to as the recovery length. Dai and colleagues show that the recovery length provides an indication of the resilience of the landscape pattern (Fig. 1).

The proposal to use recovery length as a resilience index is in contrast to most research on resilience indicators, which has used time series without spatial information², such as populations of fish, density of grasses, or algae concentrations in a lake. However, high-resolution time series are rare in ecology and may not be available for crucial ecosystems when managers need to make decisions. Spatial snapshots of resilience offer unique advantages³: they do not require intensive time series, and they may often be reconstructed from archives of aerial photos or satellite images.

To demonstrate the usefulness of recovery length, Dai *et al.* designed a system of yeast cultures that were physically linked and that exhibited alternate stable states of high or low

cell concentration, to represent patches in an ecosystem. In their experiments, the proportion of the liquid culture medium replaced each day (the dilution factor) had a critical threshold. At a low dilution factor, the yeast concentration of a patch was at the high steady state. As the dilution factor was gradually increased, the yeast concentration of the patch fell smoothly until the threshold dilution rate was reached, and then fell sharply to the low steady state. Thus, the gradual increase in dilution rate from a low value erodes the resilience of the system until the threshold is reached and the yeast population collapses.

The experimenters introduced a ‘bad patch’ (with a high dilution factor and therefore a low yeast concentration) into a series of linked cultures with identical dilution factors and yeast concentrations near the high steady state. As distance away from the bad patch increased, the yeast concentration increased gradually towards the high steady state (Fig. 1). The distance required for the yeast population to recover to the high steady state is the recovery length. As the dilution factor, and therefore the resilience, of the entire series of cultures declined, the recovery length increased.

Previous studies have shown that populations become more variable and recover more slowly from disturbance as resilience declines^{3,4}. But Dai and colleagues demonstrate that these indicators of resilience are dampened by movements of organisms between patches. Furthermore, their results indicate that the influence of a patch on its neighbours

becomes more widespread as resilience declines (Fig. 1). So, as resilience decreases, the effects of a bad patch spread farther from the epicentre. Similar effects are known from spatial models of populations subjected to harvesting⁵. Increases in recovery length may also be related to the decreasing abundance of large patches, as occurs in real landscapes when overgrazing or climate change transforms grasslands into deserts⁶.

This study and others^{7,8} demonstrate how laboratory experiments can connect model studies of resilience to real-world field applications. Simulation models are rapidly expanding our knowledge of the situations in which resilience indicators can or cannot be used, and of the statistical challenges of measuring resilience in specific situations. However, few field experiments use manipulated and reference ecosystems to evaluate resilience indicators⁹. We need intensive high-quality data collected in multiple ecosystems for many years before we will be able to measure resilience at the scales needed for ecosystem management.

Dai and colleagues’ results suggest that assessments of recovery length may be a powerful approach for determining resilience in large-scale field studies. According to their findings, in resilient ecosystems, a patch of unusually good or bad quality created by experimenters should have limited spatial influence. But in an ecosystem close to collapse, a patch of unusual quality should have widespread effects. Instead of collecting detailed time series of population densities through laborious field work, researchers can assess resilience by measuring recovery length in maps derived from remotely sensed data at just a few time points.

Thresholds for the collapse of harvested populations, the degradation of rangelands, toxic algal blooms in water supplies, species invasions and population extinctions will continue to challenge ecologists and natural-resource managers. We will never eliminate surprises. But recovery length may provide a tool that allows us to steer away from some thresholds before they are crossed. ■

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