

niche space — by dispersal to a new region or by the evolution of new ways to make a living — an initial flurry of speciation fills up an initial set of niches, but then new species become established only when others go extinct or new niches are created⁸.

Such an ecological-demand model (in contrast to evolutionary supply) also fits many evolutionary trees well³, and Price and colleagues' data on songbirds tally with this story (Fig. 1). Other data from the region suggest that recent ecological opportunity may be linked to changes in elevation, and Price *et al.* indeed find that close relatives differ most often in the elevation at which they live. The well-known pattern of highest species richness at mid-elevations⁹ is, in their data, associated with more food (and so more niches) rather than with more speciation. And songbirds span a greater range of sizes and shapes at species-poor high elevations, perhaps owing to release from competition with other groups of birds that could not establish themselves.

There is little question that an ecological-demand model of biodiversity offers up a grand narrative: nascent species arise in ample supply as isolated populations, but these expand their ranges and fill landscapes only if, and only when, those landscapes have ecological room for them. Many new species might therefore wither on the vine and never reach this expansion phase. This model implies a decoupling of the rate of speciation from the rate of subsequent establishment, a novel pattern that has recently been documented for flies and birds¹⁰.

An ecological-demand model also raises several questions. Evolutionary biologists have long appreciated that close relatives compete strongly¹¹. However, we have only recently re-appreciated that speciation is often intimately linked to diverging ecologies¹². Therefore, to evaluate the ecological-demand model, we need to know the relative contributions of ecological¹³ and non-ecological speciation¹⁴ to biodiversity production. And, given that the model suggests that the number of species in a group is related to niche availability¹⁰, we need to understand both why there are more niches for some groups (say, birds) than for others (say, mammals), and whether it is really true that, at any one time, many landscapes are full to the brim with biodiversity. ■

Arne O. Mooers is in the Biology Department and the Human Evolutionary Studies Program, Simon Fraser University, Burnaby, British Columbia V5A1S6, Canada. e-mail: amooers@sfu.ca

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ECOLOGY

Diversity in the afterlife

Field experiments that varied the composition of both plant litter and the organisms that break it down have revealed that, across ecosystems, lower biodiversity slows the rate of litter decomposition. [SEE LETTER P.218](#)

JENNIE R. MCLAREN

Despite our increased awareness of biodiversity loss, and attempts to respond to it, the global rate of species extinction does not seem to be slowing¹. Concern about how these losses may affect the way that ecosystems function has led to decades of experiments looking for connections between the properties of ecosystems and the numbers and types of species that live in them. Using field experiments and meta-analyses, ecologists have determined that decreased diversity reduces the efficiency of resource capture by communities and the conversion of those resources to biomass². Most biomass created by plants is not consumed by herbivores, but becomes 'litter' after a plant dies. Do the effects of diversity die with the plants? On page 218

of this issue, Handa *et al.*³ suggest that the answer is no, by showing that both the diversity of dead plants and the diversity of organisms that decompose them contribute to determining how quickly this material is recycled back into ecosystems.

Although experiments and meta-analyses have given us confidence in our predictions of the effects of mixing together living plants, experiments in which different litter types are mixed rarely show predictable results^{4–6}. Meta-analyses of these studies have been limited by different experimental designs, site-specific effects and the potential influence of the type rather than the number of species. Handa and collaborators attacked this problem using a series of coordinated field experiments, at sites ranging from the sub-Arctic to the tropics, in which they manipulated the diversity of both

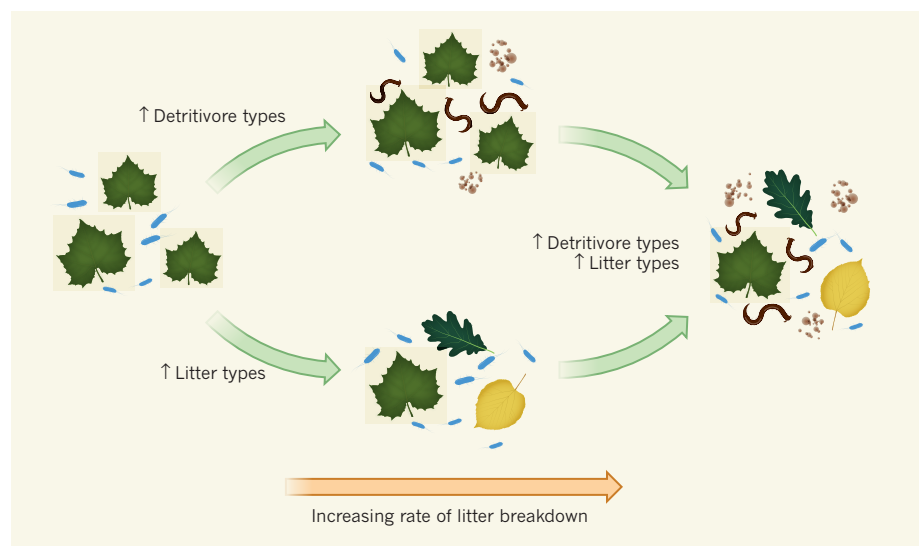


Figure 1 | Composition and decomposition. Handa *et al.*³ show that increasing the diversity of either plant litter or detritivores — invertebrates and microorganisms that break down litter — independently increases rates of litter breakdown. Simultaneously increasing both litter and detritivore diversity results in the largest increases in decomposition rate.

plants and detritivores — the invertebrates and microorganisms that break down litter. They found that a reduction in the diversity of either slows the rate at which litter is decomposed, regardless of the location of the experiment (Fig. 1).

Decomposition rates are an important determinant of the global carbon budget, affecting not only the incorporation of vegetation carbon into soils, but also the early stages of its release back to the atmosphere. That Handa *et al.* found effects of diversity on this process across biomes and ecosystems suggests a remarkable consistency in the consequences of biodiversity loss.

The authors manipulated detritivore diversity by varying the types of container the litter was decomposed in, and thus the organisms that could access and break down the litter. They show that the diversity of these organisms had even more influence than the composition of the litter community itself — the more types of detritivore, the faster the litter was decomposed. This finding provides experimental support for the results of a meta-analysis⁵ that concluded that the effects of consumer diversity on decomposition are generally more important than the effects of resource diversity.

Handa and colleagues' study is also one of the first to provide evidence for a potential mechanism driving the effects of higher litter diversity: the movement of nitrogen between different litter types. Laboratory studies had previously shown that such nitrogen movement was possible⁷, but whether it could occur in natural settings, and whether it would lead to changes in decomposition, was unknown until now.

Although nitrogen movement between leaves had been predicted to follow a simple gradient — from leaves with more nitrogen to leaves with less — it may instead be driven by carbon quality. If microbes grow quickly on litter from plants with high-quality carbon, this would increase the microbes' need for nitrogen, and when it is not available locally they may access it from the neighbouring litter. Handa *et al.* found evidence for nitrogen movement between litter types across biomes and ecosystems, and always between the same two litter types (from nitrogen-fixing litter species to rapidly decomposing ones). This is an exciting result that will increase our ability to predict the effects of biodiversity loss on carbon cycling and storage.

However, there is still no direct evidence for nitrogen translocation — in the latest experiments, it was inferred from patterns in nutrient loss or gain as the litter decomposed. The researchers report that when the nitrogen-fixing and fast-decomposing litter species are decomposed together, the amount of nitrogen present in one goes up while the amount in the other goes down, which is best explained by nitrogen moving between species. But it is possible that the nitrogen

moving into the litter is coming from elsewhere, including the surrounding soil. Given that the predictive power of Handa and colleagues' results hinges on knowledge about underlying mechanisms, a key next step will be to confirm the implied mechanism with direct tests in the field. One possibility would be to perform experiments using litter with radiolabelled nitrogen in the field, which have so far been done only in the lab.

We are increasingly aware that understanding the impacts of biodiversity loss requires recognizing that not all species are at equal risk of extinction⁸. The identity of species lost has been shown to have large effects on plant productivity⁹ and decomposition³, which results in a range of potential outcomes for different extinction scenarios. Thus, being able to accurately predict the effects of species loss at a broader scale will require both generalizable rules linking certain types of species to the effects of their loss, and knowledge of the mechanisms that cause those effects.

Handa and colleagues' study brings us closer to that goal by providing three things: general patterns linking litter and detritivore diversity

to decomposition; evidence for a mechanism driving that link; and evidence that these patterns and mechanism are the same regardless of whether they occur in an Arctic stream or a forest in the tropics. With this information in hand, we can strive towards linking patterns to realistic extinction scenarios, and thus predict probable outcomes of biodiversity loss. ■

Jennie R. McLaren is in the Department of Biological Sciences, University of Texas at El Paso, El Paso, Texas 79968, USA.
e-mail: jrmclaren@utep.edu

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STRUCTURAL BIOLOGY

Action at a distance in a light receptor

A tour de force of X-ray scattering has yielded structures of a phytochrome photoreceptor in its dark and illuminated states, showing how localized protein refolding magnifies a light signal to form a cellular message. [SEE LETTER P.245](#)

ANNA W. BAKER & KATRINA T. FOREST

Sensor proteins allow organisms to perceive and appropriately respond to environmental changes. They are molecular machines comprised of sensory domains and effector modules; a specific signal is received by the former and communicated to the latter through structural changes, creating an output activity that directs a cellular response. Phytochromes are dimeric sensor proteins that specifically absorb red and near-infrared light using a covalently tethered chromophore molecule housed in a light-sensitive (photosensory) core. In this issue, Takala *et al.*¹ (page 245) demonstrate how visible light is interpreted and spatially magnified by the phytochrome dimer in a chain reaction that uses key features of the protein's three-dimensional structure.

Phytochromes regulate most of the responses of plants to light, including germination, flowering and shade avoidance, and are thus fundamental to agriculture². They are also

widespread in microbes³, and phytochromes found in cyanobacteria are thought to be ancestors of those in plants². The proteins signal by switching between two stable conformations, which correspond to the dark and illuminated states. Absorption of light by the chromophore alters a local network of hydrogen bonds and van der Waals interactions, and ultimately induces the illuminated conformation.

How these minute changes (of the order of ångströms) are transferred through the protein to regulate the distant effector domain is a long-standing puzzle. One proposed model, also applicable to blue-light receptors and sensors that react to chemical signals, involves the rotation of central helices connecting the sensory and effector modules⁴. In phytochromes, a structural element known as the tongue also spans the two modules and is likewise expected to be involved in signal transduction⁵.

The inherent dynamism of the dark and illuminated states confounds structural studies of phytochromes. Several dark-state crystal