mic low-velocity zone (LVZ) (*5*). The question is whether this LVZ is weak or viscous enough to be consistent with the geodynamical property required for the asthenosphere (*6*). A further question is how the gradual change in temperature and pressure with depth can cause the observed large seismic-velocity reduction near the base of the lithosphere. This observed sudden drop in the seismic velocity around a depth of 50 to 100 km beneath the ocean is called the Gutenberg (or simply G) discontinuity, named after Beno Gutenberg who discovered the presence of the LVZ. The G separates the high-velocity oceanic lid from the LVZ; it is sometimes referred to as the lithosphere-asthenosphere boundary (LAB) because it invokes the idea that it is the boundary between strong lithosphere and weak asthenosphere (see the figure).

There are several ingredients that can make mantle rocks weaker: a small amount of melting (*7*) or water (*8*), and the size reduction of mineral grains. Among them, partial melting is the most effective for producing a sharp and large velocity drop at the G discontinuity, although the presence of water itself enhances melting. As the presence of a small amount of melt also lubricates the boundary (*9*), some argue that it even defines the LAB. In finding an intermittent G discontinuity beneath the Pacific, as distinct from the conventional view of a ubiquitous LVZ, Schmerr argues that a large amount of melt may exist in regions of the LAB where recent volcanism or melt production is known. As few G discontinuities have been observed where no volcanism exists, additional mechanisms are invoked—small-scale convections or mantle upwelling—that regionally enhance the discontinuity. However, as the reported properties of the G discontinuity show large scatter (*1*–*4*), further investigation is required. If we could map the G discontinuity beneath the entire ocean with accuracy, then we might be able to understand the enigmatic asthenosphere.

One of the key properties of the asthenosphere that is not well elucidated from both observational and theoretical standpoints is the strong seismic anisotropy known to exist in the LVZ (*10*, *11*). Seismic anisotropy is a polarization-direction dependence of seismic wave propagation that reflects the deformation history of mantle rocks. At present, we have neither a model of the asthenosphere that fully accounts for the observed properties of seismic anisotropy, nor do we have a well-constrained anisotropy structure of the LVZ. Thus, new sea-

floor observations and new analysis techniques combined with a large amount of seismic data from global land-based networks will be important to refine our understanding of the asthenosphere.

Plate tectonics started as a theory to explain the origins of the oceanic basin by investigating its shallowest part, leaving the deeper part of the lithosphere or lithosphere-asthenosphere system behind. Geophysical exploration of the ocean in the past several decades has focused on tectonically active areas, such as subduction zones, hot spots, and mid-oceanic ridges. Although these studies have elucidated the active part of the Earth's processes, the importance of normal, or tectonically inactive, oceanic areas, where the underlying structure may offer a textbook view of the deep mantle, might have been underestimated. Planned multidisciplinary ocean-bottom geophysical observations of the normal Pacific Ocean may finally shed light on the enigma of plate tectonics.

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ECOLOGY

Keystones in a Tangled Bank

Thomas M. Lewinsohn[1], Luciano Cagnolo[2]

Ecological network studies highlight the importance of individual species to community conservation.

In the past decade, ecologists have increasingly applied complex network theory (*1*, *2*) to ecological interactions, both in entire food webs (*3*) and in networks representing ecological interactions, especially those between plants and their animal pollinators or seed dispersers (*4*). How important are individual species to the maintenance of such ecological networks? On page xxxx of this issue, Stouffer *et al.* (*5*) analyze terrestrial, freshwater, and marine food webs to infer the contributions of individual species to network stability. In a related field study on page yyyy of this issue, Aizen *et al.* (*6*) explore plant and pollinator webs on a landscape scale. Using a different field study design, Pocock *et al.* (*7*) recently focused on a local community in which several webs of different kinds of interactions and organisms form a composite network.

Stouffer *et al.* decomposed previously studied food webs into groups of three species linked by interactions (see the figure, panel A). Such species triads can form 13 differ-

ent configurations or motifs that may be differentially represented in networks (*8*). Each species can belong to several motifs in a food web. The authors propose that most species tend to occupy preferentially certain motifs, giving them distinctive "motif profiles."

Previous simulation studies have shown that each trophic motif contributes to either an increase or a decrease in the probability of community persistence (*9*). Combining their findings with these previous observations, Stouffer *et al.* find that each species or entity can be assigned a probability of increasing or decreasing the persistence of a community to which it belongs. Families or higher taxonomic entities tend to occupy similar motifs across different communities, which suggests that they also have invariant effects on the future persistence of a community.

Aizen *et al.* analyzed flower visitation webs in 12 isolated hills of varying size in the Argentinian Pampas, 400 km south of Buenos Aires. They recorded 268 species of plants and insect flower visitors in standardized field surveys. The number of interactions decreased from larger to smaller hills, at a higher rate than expected from the well-established species-area relation (*10*). What could cause these interaction losses?

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To address this question, the authors related two attributes of an interaction within each hill—the local frequency of a plant-visitor interaction, and the degree of generality of the partnered species—to the ubiquity of that interaction across all hills. As the networks shrink, visitation links tend to concentrate more and more on the interaction core of highly connected generalistic species, a "master hub" of species links (see the figure, panel B). However, a further result was unexpected. Several interactions that did persist on smaller hills shifted away from the core to a peripheral position in the network. Species partnered in those interactions have fewer interactors in depauperate communities.

Pocock *et al.* assembled a "network of networks" from several studies within a mixed-use 125-ha organic farm in southwest England. The farm mainly comprises fields cultivated with pastures and several crops in rotation; less than 10% of the area consists of noncultivated habitats, including small woods, hedgerows, and field margins. The authors inventoried local species including all native and cultivated plants, samples for a suite of vertebrates and insects, and their parasites and parasitoids. They linked 101 plant species, including six crops, to 459 animal species in 11 networks, whose interactions were either observed or inferred from published records.

In contrast to other studies, the networks assembled in this agricultural ecosystem not only comprise different kinds of organisms but also span several interaction modes, such as herbivory and parasitism (which are antagonistic), and floral visitation and granivory (which are mutualistic). Pocock *et al.* evaluated the vulnerability of each network to disturbance. Simulating the removal of plant species in many different sequences, they evaluated their cumulative effect in each network by the extent of ensuing animal loss (starred species in figure panel A). Flower visitors and insect plant feeders were most sensitive to plant species loss; vertebrate seed feeders and parasitoids suffered far less. Furthermore, different networks did not covary substantially in their dependence on plants, except for sets of parasites and parasitoids and their respective hosts, which channel the effect of plant removal to the
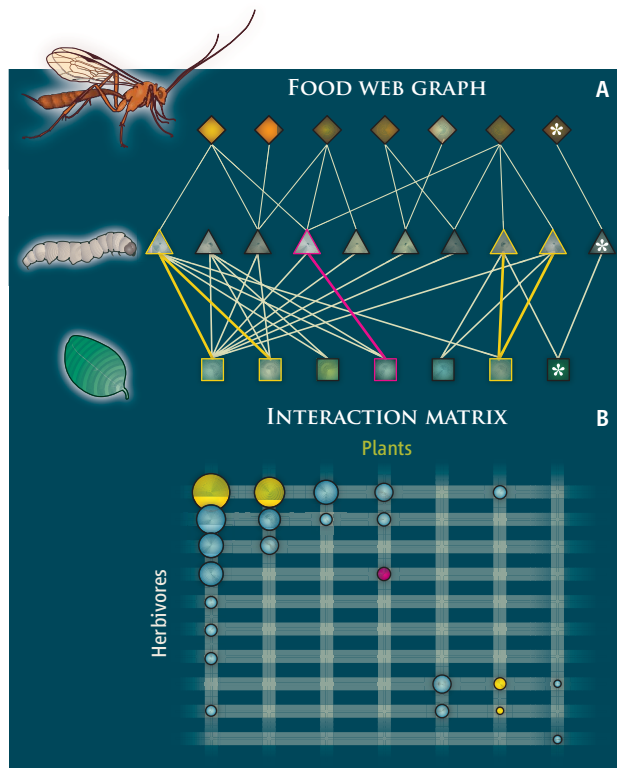
Species interaction networks. (**A**) A food web graph (*14*) with three trophic levels (plants, herbivorous animals, and parasites or parasitoids). Generalist species have more connections than specialists (from left to right), and this web has a nested structure. Stouffer *et al.* decompose entire food web networks into three-species motifs; two example motifs are highlighted in yellow. Pocock *et al.* simulate potential extinction cascades, provoked by the loss of a plant, as illustrated by the starred species on the right. (**B**) Plants and herbivores from the upper figure are shown as a matrix (*14*). Occupied cells are interaction links; the red ball corresponds to the red link in panel **A**, and the yellow balls to the example motifs highlighted in yellow in panel **A**. In this representation, symbol sizes can have different meanings; in Aizen *et al.* they represent the ubiquity of each interaction across all hills. As Aizen *et al.* show, some core interactions (top left corner) from the largest communities lose importance in depauperate communities, being shifted downward and/or to the right in the interaction matrix.

higher trophic level. In each network, different sets of plants were most important; however, some plants—keystone species (*11*)—are critical to the maintenance of animals in several networks.

The three studies all strive to assess the importance of individual species to the maintenance of a community, but use different approaches to do so. Pocock *et al.*, assuming the primacy of bottom-up effects, projected the domino effects of the loss of each plant species on associated animals. Stouffer *et al.* appraised the value of every species or entity in complete webs by a more elaborate route, which relies on correlating membership and position in particular motifs with the effect of including that motif in model communities. Their simulations enabled the projection of dynamic consequences of removal or addition of each network component. Aizen *et al.* compared sites and communities of differ-

ent sizes to assess network changes directly, without the need to simulate species removals. By focusing on interactions rather than species, they evaluated changes in community integrity either by loss of interactions or by their displacement from the core of highly connected species to more peripheral positions.

The keystone components—those critically important to the organization and maintenance of communities (*11*)—identified by Pocock *et al.* are plants; in Stouffer *et al.* they are certain taxa according to their preferred positions in networks; and in Aizen *et al.* they are interactions rather than organisms. In focusing on these different entities, practical recommendations derived from these studies will accordingly emphasize distinct aspects of community organization.

Are these results readily applicable to the conservation and management of ecosystems? Although the authors endeavor to provide advice, these are early steps. For instance, as Pocock *et al.* note, farmers are unlikely to adopt enthusiastically the conservation of farm weeds for their keystone conservation value, unless ecosystem services (such as crop pollination or enhanced control of crop pests) are shown to be improved by these measures. The spatial scale for management of keystone components must also be considered; conservation measures are unlikely to be effective at scales smaller than the landscape or regional level.

More broadly, if Stouffer *et al.*'s results are validated by further studies, they raise hopes of foretelling a community's capacity of persistence from its taxonomic profile alone—a triple jump indeed in ecological prhediction. However, other recent results suggest otherwise. A regional study in Finland (*12*) showed that network attributes were far more resilient to habitat isolation and fragmentation than was species composition itself. It would be interesting to find out whether motif profiles were also preserved in this case.

The rich variety of results from different approaches shows their individual and complementary value. However, detailed and comprehensive data sets are certainly the scarcest and most critical resource for quantum advances in understanding the dynamics of ecological networks. Pocock *et al.* were able to resort to the large store of recorded

information in the UK to build several networks. In most places, however, these have to be built from scratch, as was done by Aizen *et al*. This requires sound design and planning and is resource-intensive, but it is feasible even in the most difficult conditions, such as lowland tropical rainforests (*13*), and the returns are highly rewarding. Indeed, such data are essential for building a sound bridge between species lists and ecosystem functions—a key priority in ecology.

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BOTANY

How Plants See the Invisible

Plants can sense ultraviolet light with a photoreceptor that only contains standard amino acid side chains.

Kevin H. Gardner and Fernando Correa

Light is a key stimulus for biological function, controlling movement, gene expression, development, circadian clocks, and many other activities across virtually every form of life. This regulation is achieved by families of photosensory receptor proteins, each of which converts light of different wavelengths into biochemical signals that can control biological function. This conversion is well understood for photosensors sensitive to visible light (wavelengths λ = 400 to 700 nm), but far less is known about photoreception outside this range. On page xxxx of this issue, Christie *et al*. (*1*) elucidate the mechanism by which plant receptors detect light in the middle of the ultraviolet (UV) portion of the electromagnetic spectrum.

Visible-light photosensors must use small-molecule chromophores such as flavins, retinals, and linear tetrapyrroles as integral parts of their sensory function (*2*). Unlike the 20 natural amino acids, these molecules can efficiently use visible light

to undergo photochemical changes, including bond isomerization and addition. These configurational changes trigger allosteric changes in the surrounding protein structure, often affecting interactions between the photosensor and downstream effector domains.

However, plants also use other parts of the electromagnetic spectrum. Forty years ago, Hahlbrock and Grisebach showed that plants irradiated with UV light produce sunscreen-type protective compounds, among other responses (*3*). The discovery of components in a plant signaling pathway triggered by UV-B (λ = 280 to 320 nm) (*4*, *5*) showed that the response is not a result of a general trigger such as DNA damage, but rather is specific to UV irradiation.
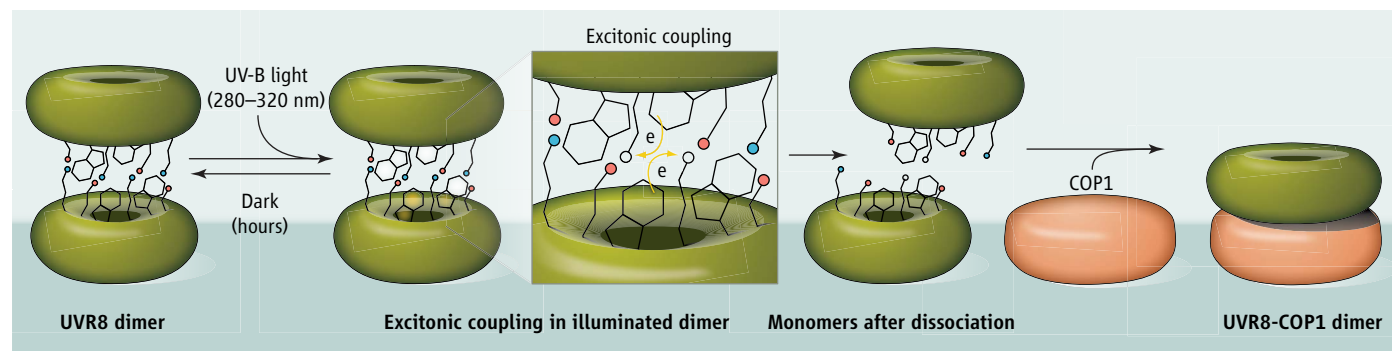
How do plants use these proteins to "see the invisible" (*6*)? Christie *et al*. provide an elegant answer to this question. They study UVR8, a component of the UV-B response pathway in *Arabidopsis thaliana*. UVR8 was previously identified as an essential component of the plant UV-B response (*4*, *7*) and exhibits several hallmarks of typical photoreceptors, including a light-dependent interaction with another protein partner (COP1) in the same signaling pathway (*7*).

The central role of UVR8 as the long-sought UV-B photoreceptor was cemented last year when Rizzini *et al*. (*8*) showed that UVR8 undergoes a light-dependent conversion from a dark-state dimer to a lit-state monomer that can interact with COP1. In contrast to all other known photoreceptors, UVR8 was found without any exogenous chromophore. Noting that UVR8 was enriched in aromatic residues with UV-absorbing side chains, the authors hypothesized that several tryptophan residues, predicted to be adjacent to each other in a UVR8 model, might play a critical role in photosensing. Mutating several of these residues to phenylalanine led to defects in light-dependent UVR8 signaling; however, key aspects of the mechanism remained unclear.

Plant UV-B photosensing. UVR8 is a doughnut-shaped molecule that forms a stable dimer in the dark state through a network of salt bridges and aromatic side-chain interactions. Christie *et al*. (*1*) show that excitation of tryptophan residues by UV-B radiation results in the donation of electrons from the aromatic clusters to nearby arginine residue(s), leading to charge neutralization and concomitant dimer dissociation. Once monomeric, UVR8 binds to the partner protein COP1, continuing the signaling pathway.

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UVR8 dimer — UV-B light (280–320 nm) — Dark (hours) — Excitonic coupling — Excitonic coupling in illuminated dimer — Monomers after dissociation — COP1 — UVR8-COP1 dimer

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