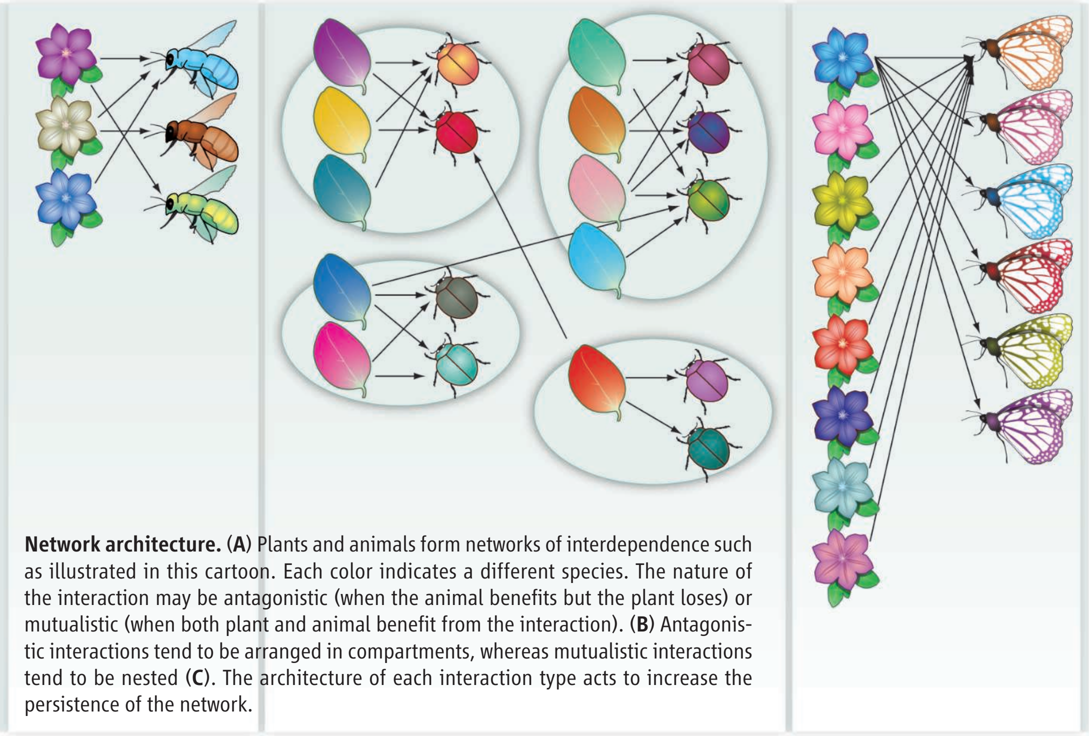
ECOLOGY

Structure and Dynamics of Ecological Networks

Understanding the architecture of species relationships may help predict how ecosystems respond to change.

Jordi Bascompte

Ecologists have a long tradition of studying how species interact. Almost all of this work, however, has focused on networks involved in a single type of interaction. For instance, ecologists have studied either "antagonistic" interactions, such as those in who-eats-who food webs, or, more recently, mutually beneficial interactions, such as those between flowering plants and their insect pollinators. Very few studies have embraced both (*1*–*3*), leaving a key question: To what degree do different kinds of interactions lead to ecological networks with different structures? The answer is crucial to understanding the suite of ecological, evolutionary, and coevolutionary processes that shape these networks and how they may respond to future changes. On page 853 of this issue, Thébault and Fontaine (*4*) take an important step forward by comparing the structure and dynamics of antagonistic and mutualistic networks.



Network architecture. (**A**) Plants and animals form networks of interdependence such as illustrated in this cartoon. Each color indicates a different species. The nature of the interaction may be antagonistic (when the animal benefits but the plant loses) or mutualistic (when both plant and animal benefit from the interaction). (**B**) Antagonistic interactions tend to be arranged in compartments, whereas mutualistic interactions tend to be nested (**C**). The architecture of each interaction type acts to increase the persistence of the network.

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To understand community dynamics, ecologists must address two main issues. First, they must describe the architecture or structure of ecological networks. Second, they must illuminate how the architecture influences species extinction or persistence. The first task rests on countless hours of careful field work and imaginative statistical analyses. The second relies on analyzing mathematical models that encapsulate network dynamics. Thébault and Fontaine beautifully relate both structure and dynamics in a single, integrative study. To put their contribution in the best perspective, it helps to step back and consider some classic and more recent results of community ecology.

Early research uncovered universal properties in the architecture of food webs, regardless of differences in species composition and network size (*5*). Parallel to this structural work, an influential paper by May illustrated that—contrary to intuition—the more complex a randomly built food web, the less stable it is (*6*). The main point of May's paper—and the reason that it continues to be influential almost four decades later—is not that complex ecological networks have to be unstable. Instead, the point is that real networks must have some contrasting, nonrandom structures that allow them to persist despite their complexity. One example of such a nonrandom pattern is "compartmentalization," or the tendency of a complex network to become organized in "compartments" characterized by a group of species interacting more strongly among themselves than with other species in the food web. A rich body of work has expanded this research (*7*) by documenting the numerous ways that the organization of food webs enables them to persist. However, this effort has focused almost exclusively on antagonistic interactions.

More recently, ecologists have turned their attention to mutualistic networks, bringing a quantitative framework to the study of coevolution in species-rich communities (*8*, *9*). This work has helped to dispel the frequently assumed view that coevolution has to lead to either highly specific, one-on-one species interactions or to diffuse assemblages that are intractable to analysis. Instead, this new generation of network studies has shown that mutualistic interactions have a "nested" architecture (*9*). In nested networks, more specialist species interact only with specific subsets of those species interacting with the more generalist species. This architecture—which researchers have compared to a set of nested Russian Matryoshka dolls—has been found to increase network robustness (*10*) and to maximize the number of coexisting species supported by these networks (*11*).

Still, the question remained: To what extent are these two types of ecological networks (antagonistic and mutualistic) arranged in different manners? To find out, Thébault and Fontaine simultaneously analyzed a large data set of both plant-pollinator and plant-

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herbivore networks (*4*). They found that the mutualistic, plant-pollinator networks tend to be organized in a nested pattern; in contrast, the antagonistic, plant-herbivore networks tend to be organized in compartments (see the figure). Thébault and Fontaine next used a dynamical model to illustrate that, as species interact, mutualistic networks tend to become more nested than they were at the beginning. Antagonistic networks, in contrast, become more compartmentalized. Finally, the authors report that these contrasting architectures are the very ones that also increase the persistence of species in each network type.

These findings present a convincing case that the empirically observed architecture of an ecological network has clear implications for how it may respond to change. There are, however, important issues that remain to be explored. One is the mechanism leading to these contrasting network architectures. One could think that because each structure maximizes the persistence of its respective network type, increasing persistence is the driving force.

This may be the case, but—as with many other interpretations in biology—a correlation does not imply causality. Some researchers, for example, have argued that the "arms race" created by the tendency of herbivores to attack less-defended plants, and the subsequent tendency of plants to counteract such attacks, can by itself lead to networks with a compartmentalized structure (*8*). Here, each compartment would represent a close group of plants and insects participating in their own arms race toward specific adaptations. This mechanism, however, is not incompatible with others, and network structure probably reflects a combination of different processes (*12*).

The ultimate approach to disentangling the role of different mechanisms would be to create an experimental setting in which investigators can manipulate network structure while keeping other variables constant. This would pave the road toward exploring how the functional traits of species, and the many services provided by ecosystems, relate to ecological network structure. We might then be in a position to assess how the web of life, and the services it supports, will respond to global change.

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CELL BIOLOGY

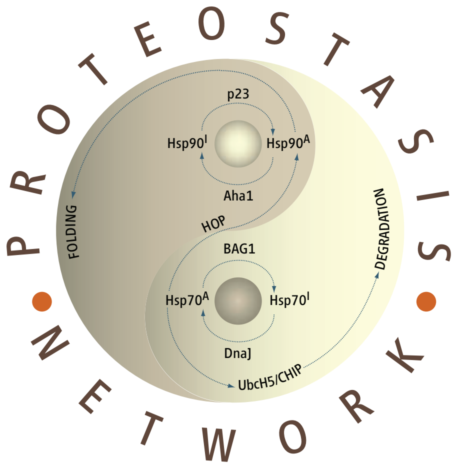
The Proteome in Balance

Cells monitor and maintain protein homeostasis by coordinating protein folding and degradation processes in multiple cellular locations.

Darren Hutt[1] and William E. Balch[1,2]

Inherited mutations and polymorphisms that alter the sequence of a polypeptide can affect its folding and stability, triggering disease at birth and during aging. A central cellular mechanism for generating and maintaining normal protein folds is the protein homeostasis or proteostasis network (referred to as the PN) (*1*). These processes sustain functional proteins as well as direct their removal from the cell during protein turnover or in response to misfolding. This "yin-yang" balance is critical for normal cellular, tissue, and organismal physiology. On page 805 in this issue, Okiyoneda *et al.* (*2*) show that the PN operates globally, constantly surveying protein folds, from co-translational insertion of proteins into the endoplasmic reticulum (ER) to removal of unstable proteins at the plasma membrane.

Okiyoneda *et al.* analyzed a mutant form of the cystic fibrosis transmembrane conductance regulator (CFTR) protein, an ion channel that transports chloride ions across mammalian epithelial cell membranes. The most prominent disease-causing mutation in cystic fibrosis is deletion of phenylalanine at position 508 (ΔF508) found in a cytosolic-oriented domain. This mutation causes an energetic destabilization that alters protein folding, targeting the mutant for removal (*3*). Whereas much work has focused on components of the PN that dictate folding and stability in the ER (*4*), Okiyoneda *et al.* have identified factors that regulate the stability of CFTR in the plasma membrane, the so-called peripheral quality control.



The yin and yang of proteostasis. Schematic representation of the balance between the folding (yang) and degradation (yin) branches of the cellular proteostasis network (PN) that globally manage protein folding in the cell in health and disease. Hsp70 and Hsp90 cycle between active (A) and inactive (I) forms by the regulatory co-chaperones shown. Hsp70/90 organizing protein (HOP) transfers proteins as shown. Prolonged binding of proteins to Hsp70 results in the recruitment of ubiquitin-conjugating (UbcH5) and ubiquitin-ligating (CHIP) enzymes that lead to degradative pathways. The balance between yin and yang pathways in human health and disease is regulated by the PN.

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At physiological temperature (37°C), ΔF508 is rapidly degraded in the ER (*3*). This mutant can be delivered to the plasma membrane at a lower temperature (26°C), but a return to physiological temperature then triggers its degradation. Okiyoneda *et al.* took advantage of this temperature-sensitive local-

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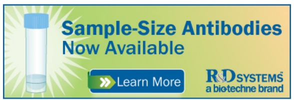

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