

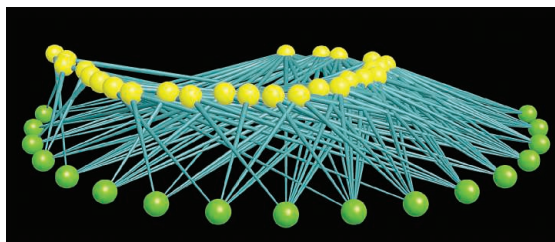
Mutualistic Webs of Species

John N. Thompson

As life has diversified over billions of years, so have the ways of extracting a living by exploiting other species. Indeed, no multicellular eukaryotic organism is capable of surviving and reproducing using only its nuclear genes and the gene products it makes. Species coopt the genomes of other species by forming mutualistic, but inherently selfish, alliances. You can grasp the central importance of mutualistic associations in the diversification of life through a simple thought experiment. Try to imagine a plant that can survive and reproduce in a real ecosystem without using, in addition to its nuclear genome, most of the following: a mitochondrial genome (to convert energy); a chloroplast genome (to regulate photosynthesis); one or more mycorrhizal fungal genomes (to improve nutrient and water uptake); the genomes of pollinators (to assist in reproduction); and the genomes of a few birds, mammals, or ants (to move seeds around the ecosystem). Each plant is part of a complex web of interacting mutualists.

One of the major challenges for evolutionary biology is to understand how species coevolve and shape complex webs of mutualistic interaction (see the first figure). On page 431 in this issue, Bascompte *et al.* (1) address an important component of this problem by asking if mutualistic interactions involving dozens or even hundreds of plant and animal species coevolve in a way that leads to a predictable pattern of links among species. They focus on some of the most visible, diverse, and quantifiable mutualistic interactions found within terrestrial communities—those between plants and their free-living pollinators and seed-dispersal agents. Some ecosystems, such as tropical rain forests, rely so heavily on these interactions that they would collapse in their absence, because plant reproduction would cease. Within these webs, it is rare for a local plant species and animal species to be so reciprocally specialized that neither interacts with other species (2). Instead, species differ greatly within webs in the number of links to other species. For example, some bee species are extreme specialists that visit the flowers of only one or two plant species, but other bee species are generalists that visit the flowers of dozens of plant species. In a previous analysis (3), these authors used network theory (4) to show that specialization within these mutualistic webs tends to be nested. In a nested web, a

Quantitative analysis of a network of plant-animal interactions reveal new organizing principles, including how asymmetric relations stabilize the coevolution of the whole network.



Species interaction web. Asymmetries revealed in the pattern of links among animal (yellow) and plant (green) species.

core group of generalists all interact with each other, but extreme specialists interact only with the generalist species. The result is a web with many asymmetries in degrees of specialization among the interacting species. In contrast, interactions between predators and prey or herbivores and plants are often more compartmentalized, forming smaller clusters within the broader interaction web (5, 6).

The new study adds additional ecological realism to these analyses. Most studies of nested and compartmentalized webs have been based on qualitative data, in which all connections between species are given equal weight. Recent studies of food webs with antagonistic interac-

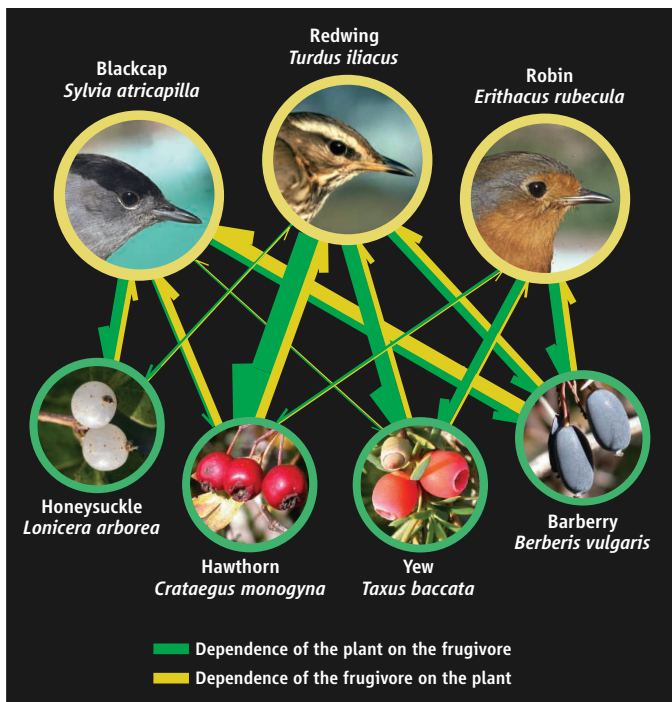
tions between species have begun to explore webs in which the connections among species are weighted by the relative frequency with which a species interacts with other species (7). In extending quantitative network analyses to mutualistic webs, Bascompte *et al.* show that the distribution of specialists and generalists within these webs is unlikely to be due to chance. Moreover, they show that asymmetries in

specialization among pairs of interacting species are the rule: Strong dependence on a particular interaction in one direction is frequently accompanied by weak dependence in the other direction. Hence, a plant might rely heavily on the seed-dispersal services of a particular frugivore species, but that same frugivore species might consume fruits from multiple plant species (see the second figure).

Using a simple model, they also show that this asymmetry in specialization could promote the coexistence of species within these interactions over evolutionary time. Complex mutualistic webs are therefore not haphazard collections of specialists and generalists. Evolution and

coevolution appear to shape these multispecific interactions in a predictable manner regardless of the exact composition of species or the ecosystem, pointing the way to a more tractable theory of coevolution within complex mutualistic webs.

Precisely how coevolutionary selection contributes to creating nested mutualistic networks built upon weak and asymmetric links among species is not yet clear. The observed differences in the structure of mutualistic and antagonistic webs, however, are consistent with what is currently known about coevolutionary selection among pairs and small groups of interacting species (8). Antagonistic coevolution between predators



Asymmetric relationships. Part of an interaction web from a montane forest in southeast Spain (1). Each interaction between frugivore and fruit illustrates two dependence values (green and yellow arrows). The relative frequency of the interaction is shown by the thickness of the arrows.

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and prey can favor escalating “arms races” among groups of interacting species, producing multispecific clusters that share some reciprocal specialization in defenses and counterdefenses. Amid these arms races, selection continually acts on prey to escape the interaction, preventing predators from incorporating an ever-increasing number of prey species into their diets. In contrast, mutualistic interactions between free-living species often favor incorporation of new species into an interaction, through convergence and complementarity of traits among interacting species. The result is a coevolutionary vortex that grows in the number of interacting species over evolutionary time. Bascombe *et al.* notably extend this general expectation from coevolutionary theory to suggest that species join networks in ways that ultimately create a persistent asymmetric pattern of specialization among interacting species.

The next step in such studies will be to identify the sequence of ecological, evolutionary, and coevolutionary processes that create this

pattern as mutualistic webs accumulate species over space and time. Some mutualistic life histories, for example, are not even possible until mutualistic webs include many species. Honeybees, which rely upon a seasonal progression of flowering among species to maintain their hives, could not have evolved until local communities included multiple plant species that flowered at different times. Identifying the evolutionary and coevolutionary processes that shape asymmetries during the assembly of complex mutualistic webs will require studies of how particular pairs and groups of species differ in their patterns of asymmetry in different biological communities.

Studies of complex mutualistic webs are part of an overall scaling up of the fields of coevolutionary biology (8) and community ecology (9) to encompass the processes shaping the diversity of life across large geographic and temporal scales. These studies are also part of a growing realization that much of the diversification of life is about the diversification of

interactions through ongoing coevolution.

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CHEMISTRY

The First Femtosecond in the Life of a Chemical Reaction

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When light initiates chemical change—such as photosynthesis in plants, or vision in an eye, or the formation of vitamin D in your skin—the first stages happen with breathtaking rapidity. Electrons in molecules can absorb a photon and rearrange in only femtoseconds (a femtosecond is 10^{-15} s). A bedrock of chemical theory known as the Franck-Condon principle assumes that such short times are so infinitesimal that for all practical chemical purposes they are instantaneous: All the atoms in a molecule remain frozen during the critical instant of electron transition. Yet quantum mechanics requires that the atoms in molecules are never truly at rest, and the removal or repositioning of electron charge initiates motion that eventually leads to chemical transformation. These earliest atomic movements have never been observed directly, because they are far too fast and too slight to detect. But this is just what the report by Baker and co-workers shows on page 424 of this issue (1). This research comes from the rapidly growing field of attoscience. An attosecond (10^{-18} s) is even shorter than the

events that initiate photochemistry, but the name has been taken over to include physical observations on time scales shorter than a single cycle of visible light, or shorter than about two femtoseconds. The specific technique used here is high-harmonic generation (HHG) in molecules illuminated by intense femtosecond pulses of focused laser light.

The report by Baker *et al.* describes and then demonstrates a new method to convert the spectrum of high harmonics into an image of the motion of molecules (such as hydrogen or methane) in the first stages of chemistry. The HHG process, in which visible or infrared laser light is converted to vacuum ultraviolet radi-

Tracking molecular motion. (Top) A laser field (black arrow) pulls an electron quantum wave (blue) away from the molecule, causing the two atoms (black dots) to separate. **(Center)** When the laser field reverses, the quantum wave smashes back into the molecule. Color represents the wave energy, with blue for fast high-energy waves and red for slow low-energy waves. **(Bottom)** The electron wave is absorbed, creating photons with energy corresponding to the wave energy. In this way, each color of light shows the molecule at a different time as the atoms move apart. Total time elapsed is about $\frac{1}{2}$ of an optical cycle, or one femtosecond.

Bombardment of reactants with high-order harmonics of a laser reveals the earliest stages of chemical reactions, which occur faster than a single cycle of visible light.

