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COMPLEX SYSTEMS

Cooperative network dynamics

George Sugihara and Hao Ye

Nested, or hierarchically arranged, mutualisms allow ecosystems to support more species than they otherwise would. But in this and other contexts, the growth of such networks could carry a heavy price.

On page 1018 of this issue, Bascompte and colleagues (Bastolla *et al.*)¹ describe how they have followed up earlier studies² of the mutualistic networks of plants and their animal pollinators. This new investigation is an intriguing enquiry into whether the particular topology of cooperative interactions accommodates greater biodiversity (network size), and it has potential applications beyond ecology to the dynamics of social and financial systems.

In the ecological networks under consideration, plants and animals compete for resources within their respective groups. But they may obtain mutual pay-offs across groups, in the form of pollination services and nectar rewards, that can offset the dynamic limits to system size determined by competition. These 'dual category', or bipartite, cooperative networks exhibit a common architecture called nestedness³, in which relative specialists — those species with few cooperative links — interact only with subsets of species having greater numbers of cooperative links. This somewhat abstract hierarchical feature gives rise to network 'disassortativity'^{2,3}, in which nodes with few connections (specialists) tend to be connected to nodes with many connections (generalists), and vice versa. (Strictly speaking, nestedness is restricted to bipartite networks, and disassortativity is a more general property of node connectivity.) Either way, this gives the network an overall appearance similar to that of the Fedwire network operated by the US Federal Reserve System for interbank payment transfers³. This network has a dense core of well-connected large institutions (generalists) fringed by a periphery of smaller banks (specialists).

How does nested mutualism affect the way systems operate? In a fully connected network in which all plants cooperate with all animals, mutualism reduces the effective competition within each bipartite class: within plants and

within animals. However, in situations in which not all mutualistic interactions are present, some cooperative links will serve to decrease competition (Fig. 1a), whereas others can actually increase it (Fig. 1b). To clarify the role of nestedness in reducing the effects of competition, Bastolla and colleagues¹ apply a 'soft mean

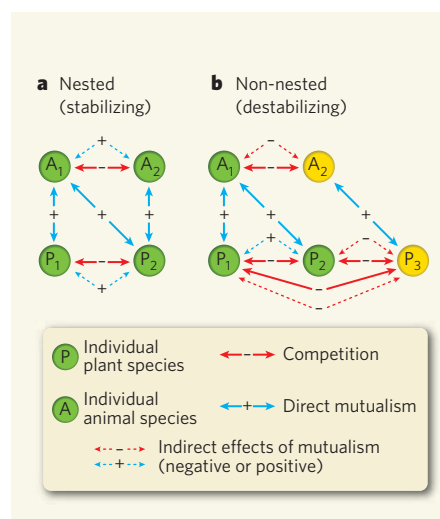


Figure 1 | Nested mutualism reduces competition. **a**, A nested cooperative network¹, in which both the specialist plant P₁ and the generalist plant P₂ interact with the generalist animal A₁. Because both plants share a mutualism with the generalist animal A₁, the competition between them is reduced. Similarly, competition between both animals is decreased by mutualism with generalist plant P₂. **b**, In a non-nested network, the specialist animal A₂ does not interact cooperatively with a subset of the species with which the generalist animal A₁ interacts. So competition between animals A₁ and A₂ is exacerbated by mutualism with competing plants. The same principles apply to competition between P₁ and P₃ and between P₂ and P₃ (amplified by their mutualism with competing animals).

field' approximation to the plant–animal interaction matrix to derive an analytical expression for competitive load. They clearly show that nested mutualism reduces overall competition for a given number of cooperative interactions, and so has a potential stabilizing effect.

Thus, whereas competition normally limits the number of species that can coexist (as tough competitive markets often tend towards monopoly), the nested cooperative models studied here reduce competition and allow the system to support more species, or higher biodiversity. This model prediction is supported by data from 56 plant–animal mutualistic networks, providing evidence that real cooperative networks with this structure attain a larger size than those that are relatively less nested.

Nestedness is not an isolated property of plant–animal communities, however, but appears in various social contexts, including the organization of the New York garment industry⁴ and as disassortativity in the topology of the Fedwire network³. Indeed, it is possible that the appearance of similar topology among diverse cooperative networks may be a result of simple shared assembly rules⁵.

A common theme among various network assembly rules^{5–7} in ecology (for food webs, for instance) is the idea of growing the network along paths of least resistance, with simple constraints that minimize competition. This is the situation in which species join the network in order of increasing specialization with minimal competitive resistance⁷ (Fig. 2). As described by Bastolla *et al.*¹, when a specialist species joins the community by interacting with a generalist species, overall competitive load is decreased. This results in a self-reinforcing nested network, in which existing generalist species gain more connections as specialist species enter the system: reduced competition, in turn, attracts more specialists.

In the case of the New York garment industry⁴, where cooperation occurs between two classes of companies — contractors and manufacturers — the establishment of a new small contractor (that is, a specialist animal) is facilitated if that company cooperates with a large, well-established manufacturer (a generalist plant). An analogous case may hold for the payment networks of banks³, where the network topology is disassortative. Here, disassortativity may arise naturally when banks seek relationships with each other that are the most mutually beneficial: for example, small banks may interact with large banks for security, lower liquidity risk and lower servicing costs, and large banks may interact preferentially with small banks in part because they can extract a higher premium for services and can in principle accommodate more risk. Simple incentive rules can give rise to self-reinforcing disassortativity.

However, the same hierarchical structure that promotes biodiversity in plant–animal mutualistic networks may also increase the risk

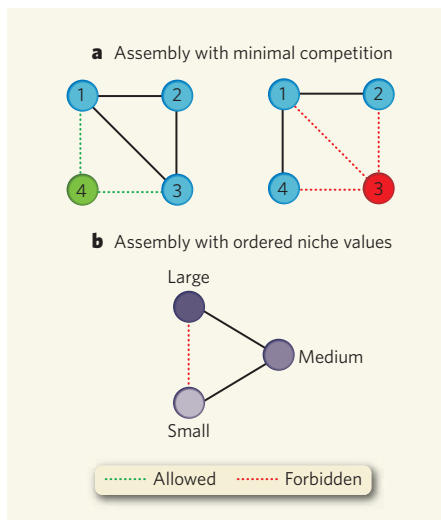


Figure 2 | Minimal assembly rules can explain network structure. **a**, An assembly rule that minimizes competition by adding specialists along paths of least resistance¹; solid lines denote existing connections. The left-hand sequence minimizes competition by adding species 4 to a single guild of competing species (1 and 3). Because it is easier for species 4 to join the network as a specialist, this is a path of least resistance. In the right-hand 'forbidden' sequence, the new species (3) must compete with two guilds of species — (4 and 1), (2 and 1) — and is not entering as a specialist. **b**, Another common minimal assembly constraint is a natural ordering in the resource set⁷, as might result from evolution⁶. The nodes are resources used by each species (here, seed sizes), and each species is represented as a line joining two resource classes. Adding a species that eats small and large seeds, but ignores middle-sized ones, violates the niche ordering (a common minimal assembly constraint)^{1,5,7}. (Graphic modified from ref. 7.)

of large-scale failures in cooperative networks⁸. Mutualism facilitates greater biodiversity. But it also creates the potential for many contingent species to go extinct, particularly if large, well-connected generalists (for example, certain large banks) disappear.

Moreover, as reported by Bastolla *et al.*¹, a strong mutualistic interaction between two species (excessively favourable selective terms) can move the system into a strong mutualistic regime; this will destabilize other weakly mutualistic species groups whose interaction strength falls below some threshold. Over time, only the strong cooperators survive, and the weakly cooperating species groups go extinct. This stylized behaviour of simple mutualistic networks possibly applies to other domains, in which strong cooperation between two agents may cause the demise of all other agents — or where, in less-stylized cases, uneven cooperative subsidy or advantage in global networks can be dangerous unless the mutually beneficial effects propagate more or less evenly throughout the network.

As a specific speculative example, consider the interdependence of the Internet auction

site eBay and the payment system PayPal. PayPal was the dominant method of payment for eBay auctions when it was bought by eBay in 2002, strengthening cooperative links between the two companies. Insofar as this simplified model applies, this duopolistic partnership would have encouraged the demise of alternative competing payment systems, such as eBay's Billpoint (phased out after the purchase of PayPal), Citibank's c2it (closed in 2003) and Yahoo!'s PayDirect (closed in 2004).

Whether Bastolla and colleagues' model¹ of structured cooperation performs the same role in other domains is intriguing but unclear. In particular, the extent to which the topology of cooperative linkages in payment networks — or more importantly, in networks of balance sheets — may increase systemic risk in the financial sector remains an open question⁹. Tackling such questions will no doubt require

mutualistic cooperation between researchers linking different competitive fields. ■

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NEUROSCIENCE

Optical control of reward

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Is it wishful thinking that the behaviour of an organism as complex as a mouse might be controlled by modulating its intracellular signalling with light?

No: this is just what researchers have achieved with an elegant technique.

Ever since the Italian physician Luigi Galvani discovered that frogs' muscles twitch when stimulated electrically, the integral role of electricity in the functioning of the nervous system has seemed clear. But there is also a growing appreciation that intracellular signalling pathways — which can interact with the extracellular environment through G proteins and G-protein-coupled receptors (GPCRs) — play an essential part in the processing of information by neurons. Deisseroth and colleagues¹ (Airan *et al.*, page 1025 of this issue) now describe a powerful technique that allows intracellular signalling pathways to be controlled through the activation of GPCRs by light. Intriguingly, by modulating specific signalling cascades in this way, the authors can control behaviour in mice.

Deisseroth and colleagues² had previously shown that naturally occurring light-activated ion channels, such as channelrhodopsin-2 (ChR2) and halorhodopsin, could be integrated into neuronal cell membranes to drive the respective activation or inhibition of electrical impulses using light. By means of this and other similar techniques^{3,4}, neuronal impulses can be regulated with unprecedented temporal, spatial and cell-type specificity. In the latest development, Airan *et al.*¹ have created chimaeric GPCR molecules that they call optoXRs. The extracellular and transmembrane portions of optoXRs (opsin) consist of the light-activated rhodopsin protein, but their

intracellular components are those of specific GPCRs. The authors focused on two main receptors for the neurotransmitters adrenaline and noradrenaline: the β_2 receptor, which couples to G_s proteins, and the α_{1a} receptor, which couples to G_q proteins. As these two classes of G protein activate signalling pathways that are mediated by different effector molecules⁵, the authors could control a wide range of intracellular signalling pathways.

Airan *et al.* first expressed optoXRs in cell lines to test the molecules' basic functionality. Depending on the optoXR expressed, they observed a robust light-driven increase in the levels of the cellular signalling molecules calcium, cAMP and $\text{Ins}(1,4,5)\text{P}_3$ — effects that are associated with activation of the corresponding native GPCRs. What's more, the levels of increase were similar to those that occurred after activation of the native receptors, demonstrating that optoXRs can potentially regulate intracellular signalling in a physiologically relevant yet precise manner via specific G proteins.

The authors next investigated light activation of optoXRs in brain slices containing neurons from the nucleus accumbens region. They report an increase in the levels of phosphorylated CREB, a protein that functions downstream of G_s - and G_q -mediated pathways. So it seems that even downstream components of these pathways can be activated by light without the need for additional cofactors, a requirement that would have limited this technology's applicability