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Why are plant-pollinator networks nested?

Mutualistic communities maximize their structural stability

By Samraat Pawar

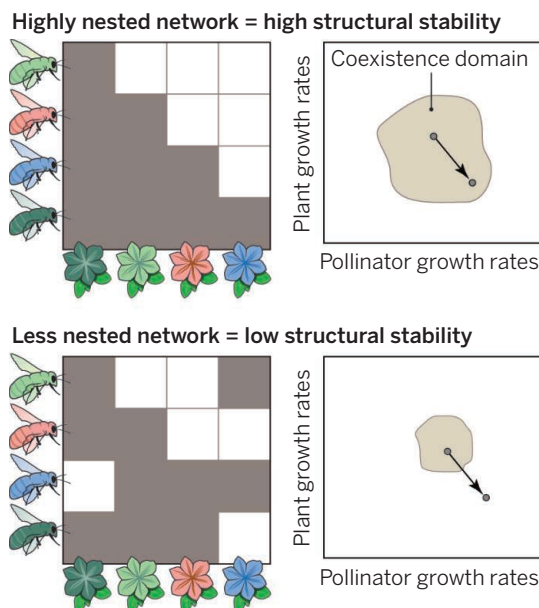
Interactions between species in a community may be mutually beneficial, competitive, or exploitative. The resulting ecological networks strongly influence the population dynamics of species (1). Nonrandom features of such networks may reflect organizing processes. For example, mutualistic networks such as plant-pollinator communities are “nested.” Specialist pollinator species visit plant species that are subsets of those visited by more generalist pollinators (see the figure). But what drives the emergence of nestedness? On page 416 of this issue, Rohr *et al.* (2) provide theoretical and empirical evidence for the decade-old idea that nestedness prevails because it stabilizes mutualistic networks.

Different studies have produced conflicting results about the consequences of nestedness at the community level (3–5). Rohr *et al.* argue that these conflicts arise because most studies have focused on how nestedness affects Lyapunov stability. This type of stability analysis is concerned with whether, for a given community, population trajectories will return to an equilibrium point after they are perturbed from it (say, due to sudden reduction in the population densities of one or more species). Instead, Rohr *et al.* study whether nestedness improves structural stability. In ecological communities, structural stability analyses aim to determine whether a network feature (such as nestedness) widens or constricts the feasible region for multispecies coexistence when biological parameters are varied (1) (see the figure).

This shift from Lyapunov stability to structural stability, originally suggested in 1974 (1), has profound implications. Any equilibrium of a community cannot be permanent because real commu-

nities are not static: Individual species may undergo changes, e.g., in their growth rate, and the species composition of the community may change, e.g., when phenotypically different individuals immigrate or emigrate. Such changes are even more likely when individuals respond to changes in environmental conditions such as temperature (6). This is why it is necessary to ask whether a system will be structurally stable to changes in biological parameters.

Rohr *et al.* investigate how structurally stable mutualistic networks are to changes in the intrinsic growth rates of species. Intrinsic growth rate is a fundamental biological parameter that determines the absolute fitness of species’ populations and varies with the metabolic rate (rate of energy use) of individuals. The intrinsic growth rate has typically been treated as a fixed parameter across all species in a community (4, 5, 7). Combining theory and data on the network



Nestedness and structural stability. According to Rohr *et al.* (1), a highly nested network (top, fully nested in this case) has a high structural stability. This means that species can coexist over larger ranges of species’ growth rates (gray shaded coexistence domain). A less nested network (bottom) will have lower structural stability (a smaller coexistence domain). Thus, perturbations to plant or pollinator growth rates can more easily displace an equilibrium point of the community out of the coexistence domain, resulting in one or more populations going extinct.

structure of 23 communities, Rohr *et al.* show that more nested mutualistic networks permit multispecies coexistence for a wider range of species growth rates: They are more structurally stable (see the figure).

Rohr *et al.*’s results imply that if a community can explore a full range of species growth rates during assembly, nestedness is the configuration most likely to be observed because of the structural stability that it imparts. This is an important step toward reconciling previous results based on Lyapunov stability. However, it remains to be shown how maximization of structural stability affects Lyapunov stability. Insights may come from studies that allow ecological networks to assemble through a stochastic exploration of species growth rate combinations (8–10). These studies have found that as communities assemble, they become more resistant to invasions by new species, likely because they have come close to the center of the coexistence domain of growth rates (see the figure). At the same time, these communities tend to be less resilient (that is, they return more slowly to equilibrium after perturbations). This fragility may explain previous results showing that nestedness undermines resilience to perturbations (4, 11).

Future work must take two critical factors into account. First, Rohr *et al.* study variations in growth rates independently of interspecific and intraspecific interaction parameters. Yet, these three sets of parameters are not independent and will covary, because they all depend on the metabolic rates of individuals. For example, both interaction and growth rates scale with body size (12, 13). Second, the methods and the results of Rohr *et al.* cannot directly be applied to consumer-resource systems and only to certain classes of competitive systems. This is a crucial limitation that future work must strive to overcome, because mutualistic systems are typically embedded in a larger, more complex network of interactions that also include competitive and consumer-resource interactions. ■

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