Biodiversity and community structure

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In natural plant communities, one finds ample examples of both competitive and facilitative interactions. The effect of a species A on another species B is said to be competitive (facilitative) if an increase in A's population size reduces (enhances) the population growth rate of B. Competition may arise if two species live in the same habitat and are therefore occupying sites at the others' expense. In turn, facilitation could happen, for example, because a plant species modifies the soil chemistry around itself in a way that makes it especially beneficial to members of another species. Is the prevalence of competitive and facilitative interactions merely a statistic associated with communities, or does it reveal other properties of interest? For instance, is it conducive to biodiversity to have either very many competitive or very many facilitative interactions within a community? In a recent study in PNAS, Losapio et al. (1) argue that the two are needed in concert. An overprevalence of certain combinations of competitive and facilitative interactions predictably leads to more plant species within a community.

Every species potentially interacts with many others. Communities can therefore be viewed as interaction networks (Fig. 1) in which each species is embedded (2). This must be taken into account when pondering the potential community-wide effects of competition and facilitation. Naively, competition may be thought of as a destructive force, hindering the coexistence of species. Things are not that simple, however, because of the principle that "the enemy's enemy is a friend." If two species are in competition and the second one is a superior competitor, it might drive the first one extinct—unless there is a third species that is also in competition with the second, keeping it sufficiently in check for all three of them to persist. Similarly, the naive logic that facilitative interactions must be beneficial for coexistence is questioned once we realize that a group of mutual facilitators might make conditions so advantageous for one another that they grow to deplete all resources, driving every other species extinct. Without

considering the broader network of interactions, therefore, our ability to draw conclusions about their effects on the community as a whole is limited. This state of affairs has meant that ecologists have invested considerable effort in gaining a general understanding of how network structure influences community persistence and stability (3, 4).

In their PNAS study, Losapio et al. (1) analyze data from 166 alpine plant communities, where they infer the effect of a species A on another species B based on whether populations of B were observed to covary with those of A within their close vicinity. A positive association was taken as evidence of a positive (facilitative) interaction, while a negative association (increase of A implying the decrease of B) was taken as evidence for competition. While this procedure may certainly raise some questions (could a positive association arise between competing species preferring similar microhabitats?), direct measurement of interactions through manipulative experiments is notoriously challenging. Therefore, such roundabout ways of inferring interaction strengths, combined with some common sense in interpreting the results, may be the best one can do. The authors then checked whether the prevalence of positive or negative interactions is related to higher biodiversity—is it true that communities with more competitive or more facilitative interactions overall harbor more species? The simple answer is no. Alone, the prevalence of these two interaction types does not correlate with the observed number of species.

This is where the authors (1) turned their attention toward network properties that are more complicated than the simple pairwise relationships of competition and facilitation. In particular, they focused on three-species interaction modules. These are obtained by isolating all possible three-species combinations from a community, and examining the structure of their direct pairwise interactions (Fig. 1). There are many different ways in which three species can be arranged

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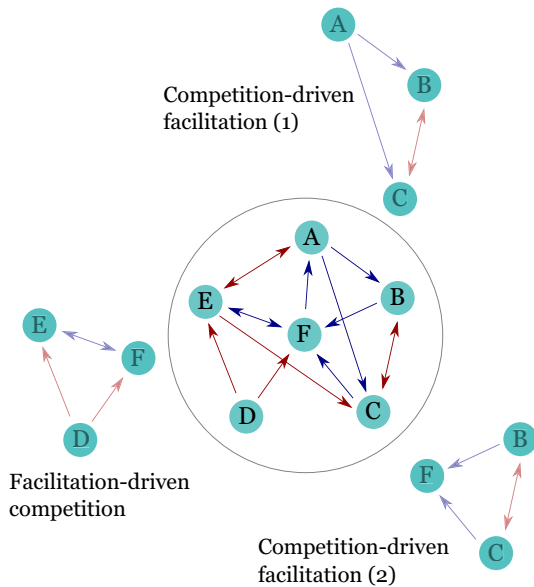
Fig. 1. Interactions in a hypothetical six-species plant community (circled graph). Species (letter-coded nodes) exert competitive (blue) or facilitative (red) influence on other species (outgoing arrows), and are, in turn, affected by them (incoming arrows). In this interaction web, any three-species subnetwork forms a network module. Three of these are highlighted in particular (subwebs outside the circle), corresponding to the key diversity-enhancing modules of Losapio et al. (1) which involve both competitive and facilitative interactions.

in a mininetwork, and, while the authors have not looked at all logically possible configurations, they have considered a subset of 13 possibilities. Of these, three turn out to be more important than the others (Fig. 1): a type of facilitation-driven competition (in which a species facilitates two other, mutually competing ones) and two types of competition-driven facilitation (two mutual facilitators either competitively affecting, or being competitively affected by, a third species). Examining the prevalence of these three small interaction modules within each alpine community, the authors find that their frequency correlates with the total number of species. Biodiversity is apparently related to these simple three-species arrangements, each of which contains a combination of competitive and facilitative interactions. In turn, the authors do not find the same positive relationship between species diversity and the prevalence of the other three-species modules they examined.

Importantly, there exist many different three-species modules with a mixture of both competitive and facilitative interactions, but only those of Fig. 1 correlate with diversity. Thus, it is not sufficient to have just any mixture of positive and negative interactions. Instead, their particular arrangement matters. This is consistent with the authors' (1) earlier finding that the raw prevalence of these interaction types has no effect on the number of species. It also provides compelling evidence that nontrivial (although still simple) structural properties of ecological networks underlie the diversity-enhancing effect. Such properties have received attention in ecology before (5), but their use remains sporadic. The study reinforces the need to look for more involved network properties, by showing that three-species modules can tell us something which mere pairwise interactions cannot.

Additionally, Losapio et al. (1) shed light on the utility of forgoing detailed information about the actual strength of each interaction and only considering their type (competitive or facilitative). Researchers from outside the field may find it quaint that ecologists frequently attempt to make sense of ecological networks based on such limited information. After all, a community where all competitive interactions are weak but all facilitative ones are strong is presumably very different from the same community where it is the other way round. Indeed, there is a debate within ecology on the usefulness of this so-called topological approach, which ignores the magnitudes of interactions and looks only at their sign (6). The fact that the authors manage to get their results without explicitly using the estimated interaction strengths indicates that there is method to the madness.

Thus, the study (1) does an excellent job of identifying and driving attention to nontrivial structural network properties that are linked to increased biodiversity in the examined alpine plant communities. Up to this point, however, this is but an empirically observed correlation between the two. Is there any evidence of a causal mechanism at hand—that is, that the prevalence of the three key modules (Fig. 1) is the reason behind increased species richness (as opposed to, e.g., the former being a statistical artifact of the latter, or the two stemming from some common cause)? To argue that there is indeed such a mechanism, Losapio et al. set up theoretical model simulations in which three species at a time were arranged in one of four ways. Three of these corresponded to the modules overrepresented in highly diverse systems. The fourth corresponded to what is known as intransitive competition (7), in which the first species competitively affects a second which affects a third which, in turn, affects the first (formed by species F–A–B in Fig. 1). Given this basic network topology, they then parameterized a simple and commonly used differential equation model of species interactions, numerically integrated them through time, and recorded how many species still persisted after sufficiently long waiting times. What they find is that the intransitive competition module (the one that was not related to species diversity in the empirical data) results in fewer of the three species surviving, on average, than in the other modules.

However, this modeling exercise supporting the notion that the three key modules in Fig. 1 are directly contributing to greater biodiversity is, in my view, a weak link in the argument. Theoretical persistence in the three key modules was only tested against one other module, intransitive competition—presumably because intransitive competition has gotten some attention in the past as a potential coexistence-promoting mechanism (7, 8). This undue focus on the intransitive competition module comes at the expense of disregarding others. Indeed, theoretical persistence may have conceivably turned out higher in those than in any of the four tested ones. But, even if the three key modules did produce greater persistence than all the others, it is unclear what that would prove. After all, the question is not whether three-species modules are better at persisting in isolation; it is whether they are able to promote coexistence when embedded in a larger network. The two are not necessarily connected (9). To use our earlier example, imagine a module in which each species facilitates the other. In isolation, such a formation may prove rock solid. However, if the mutual facilitation causes the module's species to do so well that they drive everyone else extinct, then stability in isolation will not translate to promoting diversity in a network setting. In the end, the authors' (1) model comparison is too disconnected from what may be going on in real networks to support any causal connection between module prevalence and species diversity.

Overall, Losapio et al. (1) provide compelling evidence that biodiversity and the prevalence of certain network modules involving both competition and facilitation are correlated. Furthermore,

their work drives attention to the importance of looking at higher structural network properties to understand ecological communities. However, the causal link between module frequency and species diversity remains weak. But this simply means that ecologists are not yet in danger of running out of work. There are opportunities to refine the theoretical models to rigorously argue for the diversity-enhancing effect of these modules, as well as opportunities for examining whether the same structural patterns hold in other communities apart from the alpine plant assemblages the authors have analyzed.

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