Comment on “Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance”

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Bascompte et al. (Reports, 21 April 2006, p. 431) used network asymmetries to explain mathematical conditions necessary for stability in historic models of mutualism. The Lotka-Volterra equations they used artificially created conditions in which some factor, such as asymmetric interaction strengths, is necessary for community coexistence. We show that a more realistic model incorporating nonlinear functional responses requires no such condition and is consistent with their data.

Mutualism was once thought to be inherently unstable due to unrealistic assumptions of now historic Lotka-Volterra theory. Such models (1, 2) entail changing negative signs of Lotka-Volterra competition equations to positive signs to reflect the benefits of mutualism. These models showed that mutualism is stable under limited mathematical conditions, namely, weak interaction strengths in which the product of mutualism coefficients is less than unity and/or less than the product of intraspecific competition coefficients. Otherwise, instability ensues through unbounded population growth. Extending two-species Lotka-Volterra models of mutualism (3–5), Bascompte et al. (6) repeated this result for mutualistic communities. They showed that the necessary condition for a positive steady state is \( a/b < (ST/nn) \), in which interaction strengths of mutualism \( a/b \) must be less than intraspecific competition coefficients \( ST/n \) for a community size \( mm \) of \( m \) animal and \( n \) plant species. In other words, for stable coexistence, the strength of mutualism must decline with community size for given constant intraspecific competition coefficients. Based on these theoretical results, they analyzed plant/pollinator and plant/seed disperser communities to show that interaction strengths of mutualistic networks are weak and asymmetric (hence, small \( a/b \)), and thus explain community coexistence.

Although the authors admitted to their model’s simplicity (6), we show that their results are also not robust. Including the biologically fundamental feature of nonlinear functional responses in their model removes the coexistence condition \( a/b < (ST/nn) \) that motivated their data explorations. The model with nonlinear functional responses does not require weak or asymmetric interaction strengths for community coexistence. Using the authors’ data sets, we also show that interaction strengths do not necessarily decline with community size, as predicted by their model.

More than 25 years ago, May (7) identified Lotka-Volterra models of mutualism as inadequate and unrealistically simple. Lotka-Volterra models of mutualism between two species (3) or among large groups of species (6) require some factor to stabilize interactions because their inherent linear functional responses (i.e., ever-increasing mutual benefits with increasing population densities) lead to unbounded population growth. Although many modifications can make these models more realistic, their most fundamental deficiency is not incorporating the general property that beneficial effects of one species on another tend to saturate with increasing population size of the former \( 8–10 \). By simply incorporating a Holling type II functional response into the dynamic equations employed by Bascompte et al., the mathematical condition \( a/b < (ST/nn) \) is not necessary for stability and a positive steady state occurs for the entire parameter space (Fig. 1) (11). In contrast to Bascompte et al., a more realistic model of mutualistic communities does not require weak or asymmetric interaction strengths, or declining interaction strengths with community size, to explain stability and community coexistence.

Through analyses of plant/pollinator and plant/seed disperser communities, Bascompte et al. showed that interaction strengths are weak and asymmetric. However, their results depend critically on assumptions (12) of their use of interaction frequency (dependence) as a substitute for per capita interaction strength, which gives unreliable estimates when the saturation effect (i.e., a type II functional response) is present and/or the densities of species vary greatly. Without density data, it is difficult to predict the strength of these effects. Nonetheless, even assuming that these factors are negligible, our analyses of their data refute the generality of their model prediction that mutualism strength \( a/b \) declines with community size \( mm \) [see figure S1 in (6)]. Although a negative relationship exists for plant/pollinator communities (Fig. 2), the decline in mutualism strength is not nearly as strong as predicted. The plant/seed disperser communities do not show the negative relationship (Fig. 2). Although more data are needed to evaluate mutualism strength with community size, the discrepancy observed in the plant/seed disperser data may be considered an absence of such a relationship among parameters [i.e., \( a/b < (ST/nn) \)]. Taken together with the theoretical results (Fig. 1), the negative trend observed in the plant/pollinator data is likely driven by a factor other than the Lotka-Volterra condition for community coexistence. The pursuit of mechanisms that produce weak mutualistic interactions to explain Lotka-Volterra theory for mutualism has been and remains precarious.

In recent years, important progress has been made by Bascompte, Jordano, Olesen, and others [see references in (6)] in recognizing that mutualisms form nested, asymmetric networks. Emerging empirical patterns associated with asymmetric networks, including those reported in Bascompte et al. (6), show great utility for empirical and theoretical studies of the structure and dynamics of mutualistic communities. In particular, like more traditional consumer-resource systems (13), it may well be that symmetric patterns of interaction strengths contribute to stability of mutualistic communities. However, it would be a setback if the importance of these patterns were overlooked or undermined because of their application to historically unrealistic models of mutualism that entail mathematically artificial stability conditions resulting from linear functional responses.

![Fig. 1. Phase-plane diagram showing zero-growth isoclines for mutualistic communities of plants (dP/dt = 0) and animals (dA/dt = 0) after incorporating a Holling type II functional response into dynamic equations of Bascompte et al. (6). A positive steady state for the mutualistic communities is indicated by a solid dot at the point of intersection of the two isoclines (12).](http://science.sciencemag.org/)
Fig. 2. Mutualism strength (product of the parameters describing dependence of the animal on the plant and the plant on the animal) as a function of the size of mutualistic communities. Number of species is the sum of plant and animal species described in each independent study and was used as a proxy for community size. Monotonically decreasing mutualism strength with increasing number of species was found in the plant/pollinator data (Spearman’s rank correlation test, $\rho = -0.20, P < 0.001$) but is absent in the plant/seed disperser data (Spearman’s rank correlation test, $\rho = 0.15, P = 1.0$). These statistical conclusions are robust even when the biased sample size for the larger communities is accounted for. These analyses assume that the strength of intraspecific interactions is independent of community size, because there is an absence of such data in the data sets (6), and that interaction frequency can be substituted for per capita interaction strength (12).

**References and Notes**

2. For an extensive list of examples, see references in (I4).
7. As clearly put by May, “... simple, quadratically nonlinear Lotka-Volterra models ... are inadequate for even a first discussion of mutualism, as they tend to lead to silly solutions in which both populations undergo unbounded exponential growth, in an orgy of mutual benefaction. Minimally realistic models for two mutualists must allow for saturation in the magnitude of at least one of the reciprocal benefits” [p. 95 in (3)].
11. Methods and analyses are available as supporting material on Science Online.
15. We thank three anonymous reviewers for their comments and suggestions.

**Supporting Online Material**
www.sciencemag.org/cgi/content/full/313/5795/1887b/DC1

Methods

References

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