

Comment on “Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance”

J. Nathaniel Holland,^{1*} Toshinori Okuyama,¹ Donald L. DeAngelis²

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 $\alpha\beta < (ST/mn)$, in which interaction strengths of mutualism ($\alpha\beta$) must be less than intraspecific competition coefficients (ST) for a community size (mn) 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 $\alpha\beta$), 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 [$\alpha\beta < (ST/mn)$] that motivated their data explorations. The model with nonlinear func-

tional 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 $\alpha\beta < (ST/mn)$ 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 ($\alpha\beta$) declines with community size (mn) [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., $\alpha\beta < (ST/mn)$]. 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 asymmetric 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.

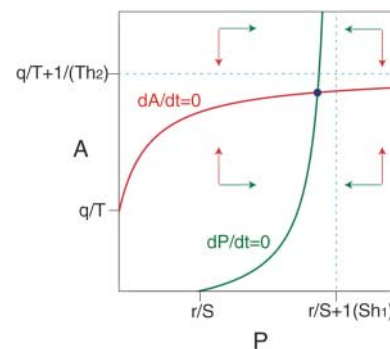


Fig. 1. Phase-plane diagram showing zero-growth isoclines for mutualistic communities of plants ($dP/dt = 0$) and animals ($dA/dt = 0$) after incorporating a Holling type II functional response into dynamic equations of Bascompte *et al.* (6). A positive steady state for the mutualistic communities is indicated by a solid dot at the point of intersection of the two isoclines (11).

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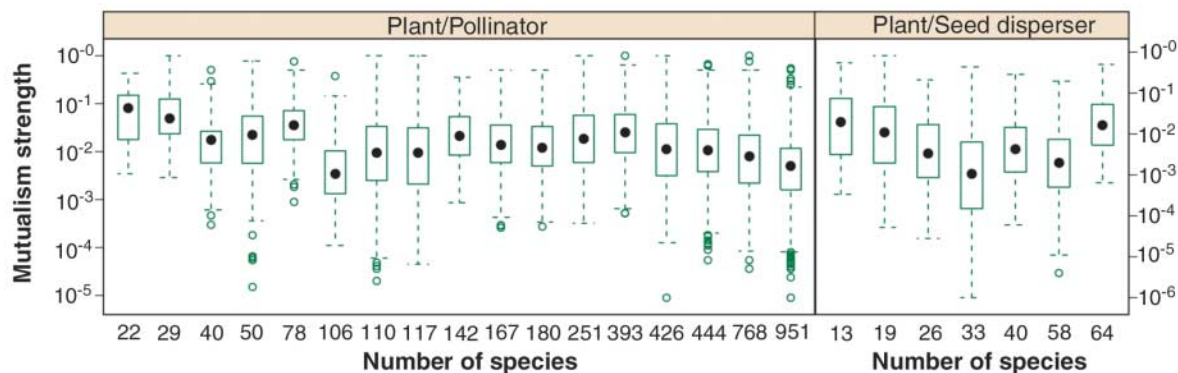


Fig. 2. Mutualism strength (product of the parameters describing dependence of the animal on the plant and the plant on the animal) as a function of the size of mutualistic communities. Number of species is the sum of plant and animal species described in each independent study and was used as a proxy 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, $\rho = 0.15$, $P \approx 1$). 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

1. G. F. Gause, A. A. Witt, *Am. Nat.* **69**, 596 (1935).
2. For an extensive list of examples, see references in (14).
3. R. M. May, in *Theoretical Ecology*, R. M. May, Ed. (Sinauer, Sunderland, MA, ed. 2, 1981), pp. 78–104.
4. R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, NJ, 1973).
5. M. S. Ringel, H. H. Hu, G. Anderson, M. S. Ringel, *Theor. Popul. Biol.* **50**, 281 (1996).
6. J. Bascompte, P. Jordano, J. M. Olesen, *Science* **312**, 431 (2006).
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)].
8. J. N. Holland, D. L. DeAngelis, J. L. Bronstein, *Am. Nat.* **159**, 231 (2002).
9. M. L. Rosenzweig, R. MacArthur, *Am. Nat.* **97**, 209 (1963).
10. D. Tilman, *Resource Competition and Community Structure* (Princeton Univ. Press, Princeton, NJ, 1982).
11. Methods and analyses are available as supporting material on *Science Online*.
12. D. P. Vázquez, W. F. Morris, P. Jordano, *Ecol. Lett.* **8**, 1088 (2005).
13. P. C. de Ruiter, A.-M. Neutel, J. C. Moore, *Science* **269**, 1257 (1995).
14. D. H. Boucher, in *The Biology of Mutualism*, D. H. Boucher, Ed. (Oxford Univ. Press, Oxford, 1985), pp. 1–28.
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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Supporting Online Material for

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This PDF file includes:

Methods and analyses

References

Supporting Online Material

Methods and analyses for Figure 1 and inclusion of a Type II functional response.

Although many modifications can be made to Lotka-Volterra models of mutualism, minimally realistic models of mutualism, whether they be of two-species or large communities, should incorporate nonlinear functional responses (1, 2). This is not just one of many complications that can be made to Lotka-Volterra models, but likely the most essential modification for any model of mutualism. In its most general application, the functional response represents how per-capita growth rate of one population varies as a function of the number of individuals or density of another population. Here, we limit ourselves to the inclusion of saturating functional responses, as they have been particularly important to the development of more realistic, mechanistic theory for predation and competition (3, 4). We modified Lotka-Volterra equations (1) - (4) of the supplemental online materials of Bascompte et al. (5) by simply incorporating a Holling Type II functional response. Rewriting equations (3) and (4) of Bascompte et al. (5) and including the Type II functional response gives the following equations:

$$\frac{dP_i}{dt} = rP + \frac{\alpha AmP}{1 + \alpha h_1 Am} - SP^2 - d_1 P \quad (1)$$

and

$$\frac{dA_j}{dt} = qA + \frac{\beta PnA}{1 + \beta h_2 Pn} - TA^2 - d_2 A. \quad (2)$$

All parameters and variables in equations (1) and (2) are as in Bascompte et al. (5), except for the addition of the second terms, which represent Type II functional responses in which h_1 and h_2 are handling times, and the addition of the fourth terms, which represent mortality rates determined by parameters d_1 and d_2 . These latter two parameters were set to zero for consistency with Bascompte et al. (5). It is important to note that, when $h_1=h_2=0$, equations (1) and (2) above are identical to equations (3) and (4) of the supplemental online materials of Bascompte et al..

Setting $dP/dt=0$ and $dA/dt=0$ and solving for the zero growth isoclines, it can be shown that as long as $h_1>0$, $h_2>0$, and all parameters are positive, then there will be a positive steady state solution (P^*, A^*) as depicted in Fig. 1, such that $r/S < P^* < r/S + 1/(Sh_1)$ and $q/T < A^* < q/T + 1/(Th_2)$. In neither case is the positive steady state dependent upon interaction strengths of α and β [i.e., mutual dependencies of Bascompte et al. (5)]. These results are not idiosyncratic to handling times, as handling times of Holling Type II functional responses are only one of many different biological factors that can lead to saturating benefits (2).

References

1. R. M. May, in *Theoretical Ecology*, R. M. May, Ed. (Sinauer, Sunderland, MA, ed. 2, 1981), pp. 78–104.
2. J. N. Holland, D. L. DeAngelis, J.L. Bronstein, *Am. Nat.* **159**, 231 (2002).
3. M. L. Rosenzweig, R. MacArthur, *Am. Nat.* **97**, 209 (1963).
4. D. Tilman, *Resource Competition and Community Structure* (Princeton Univ. Press, Princeton, NJ, 1982).
5. J. Bascompte, P. Jordano, J. M. Olesen, *Science* **312**, 431 (2006).