Response to Comment on "Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance"

Jordi Bascompte,[1]* Pedro Jordano,[1] Jens M. Olesen[2]

Mutualistic networks are characterized by weak and asymmetric interactions, which a simple model predicts will facilitate species coexistence. Holland et al. propose a more complex model and argue that coexistence is independent of mutualism strength. However, we show that mutualism strength still plays an important role in their model and that it significantly decreases with species richness as predicted.

Our study (1) analyzed quantitative plant-animal mutualistic networks and concluded that the bulk of pairwise dependences are weak and that in the few cases in which one dependence is strong, the accompanying dependence is weaker than expected by chance. We interpreted these empirical results in light of the simplest model of mutualistic dynamics, which predicts that weak, asymmetric dependences contribute to species coexistence.

Holland et al. (2) question the robustness of the prediction made by this simple model, which assumes linear functional responses. Instead, they advocate use of nonlinear, saturating functional responses and predict that weak interactions are not necessary for stability in the complex mutualisms that we examined. Here, we discuss the mathematical convergence between both models, the biological justification for nonlinear functional responses, and the statistical evidence for one model or another in light of more robust data analysis.

Holland et al. are correct that a model with Holling type II functional responses predicts species coexistence for a wide set of parameter combinations. However, mutualism strength, mediated by the handling times, still plays a role in their model. Under our criterion for coexistence, Holland et al.'s solution is bounded within a domain of plant and animal densities regardless of the value of handling time (Fig. 1, A and C). However, beyond our predicted condition for coexistence (for large enough mutualism strengths), this holds only for long handling times (Fig. 1B); the solution becomes arbitrarily large as handling times decrease (Fig. 1D). Thus, mutualism strength determines whether Holland et al.'s model converges to

our model and whether handling times are significant for the existence of a bounded coexistence point.

There is evidence for both linear and nonlinear functional responses in mutualistic interactions. For example, Howe and Estabrook (3) first suggested the existence of linear functional responses among temperate plant species and their generalist seed dispersers. Since then, linear functional responses have been documented in several studies of facultative plant-pollinator and plant-frugivore interactions (4, 5). The rationale for the type II functional responses is based on ratios of costs and benefits in highly specific pairwise dependences such as those between senita cacti and senita moths (6). Given the evidence for linear functional responses, the extreme variability in population size across species, and the trade-off between realism and simplicity, we thus opted for keeping the model as simple as possible (7).

Turning to the statistical evidence in support of one model or another, Holland et al. (2) analyzed our data sets to examine our prediction that mutualism strength must decline with increasing community size. They report a nonsignificant trend for the dispersal data set. Their test for this correlation, however, is not robust. They use a nonparametric,

rank-based Spearman coefficient that is seriously biased for two reasons. First, the values of community sizes (x variable) are not homogeneously distributed over the whole range of values. Second, using the mean or median strength value for each community size collapses an enormous range of dependence values. Both factors tend to increase the type II error rate.

We tested our prediction with a robust regression model that successfully accounts for the highly skewed strength values and weights each x value by the number of pairwise strength values. For pollination, mutualism strength decreases significantly with community size ($t = -2.13$, $P = 0.024$, df = 36). For dispersal, mutualism strength decreases marginally with community size ($t = -1.62$, $P = 0.065$, df = 12), with a significant slope evident up to the highest community size value ($t = -1.91$, $P = 0.042$, df = 10). These results reasonably support our model's prediction of a negative trend between mutualism strength and community size for both pollination and seed dispersal. Furthermore, the distribution of mutual dependence values (Fig. 2) provides a related empirical pattern that is compatible with our model's prediction.

In conclusion, Holland et al.'s model is fully compatible with our results when handling times are reduced, a situation that is likely
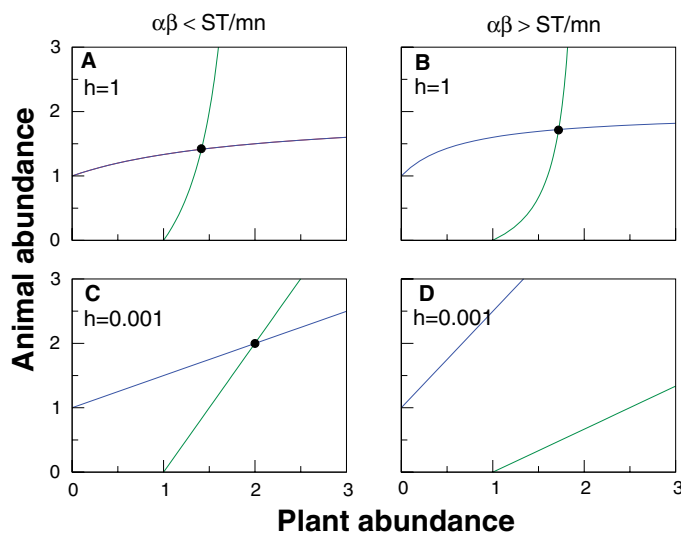

Fig. 1. The behavior of Holland et al.'s model and its convergence to the model with linear functional responses depends on mutualism strength ($\alpha\beta$). Zero-growth isoclines for plants (green) and animals (blue) are plotted in the plant-animal phase space. The dot indicates the coexistence solution. When mutualism strength is small enough (**A** and **C**), the solution of Holland et al.'s model is insensitive to handling times (h) and converges to the linear model when handling times are zero. If mutualism strength is higher than a threshold (**B** and **D**), the coexistence is bounded within a finite domain of plant and animal densities for high handling times (B) but tends toward infinity when handling times are small enough (D). Case (D) also has a finite solution, that is, the zero-growth isoclines bend and eventually intersect, but this happens for extremely large density values. Parameters are $r = q = 1$, $S = T = 1$, $m = n = 1$, and $\alpha = \beta = 0.5$ [(A) and (C)] and $\alpha = \beta = 1.5$ [(B) and (D)]. See (1) for details of the model.

[1]Integrative Ecology Group, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apartado 1056, E-41080 Sevilla, Spain. [2]Department of Ecology and Genetics, University of Aarhus, Ny Munkegade, Building 540, DK-8000 Aarhus, Denmark.

*To whom correspondence should be addressed. E-mail: bascompte@ebd.csic.es
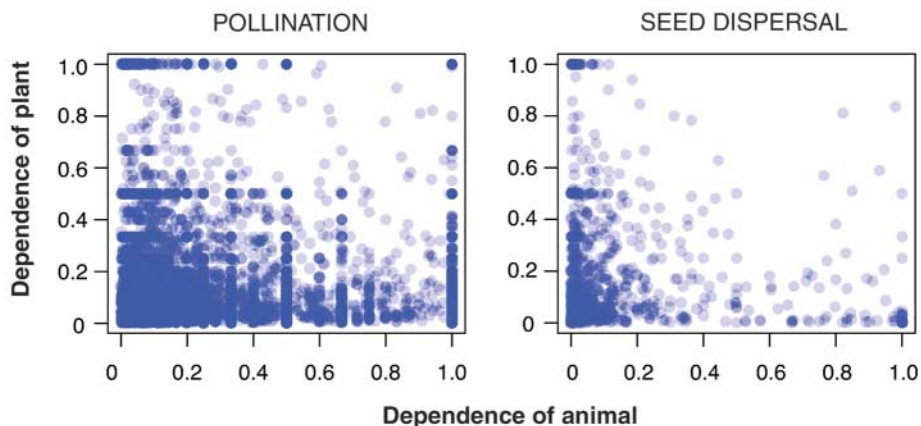
Fig. 2. Relationship between the dependence of an animal species on a plant species and the corresponding dependence of the plant on the animal. Each dot represents a plant-animal species pair. All pairs and all communities are pooled together for pollination (**left**) and seed dispersal (**right**). Note the high density around the interactions where both pairwise dependences are weak (lower left corner) and the scarcity of mutually strong, symmetric pairwise dependences (upper right corner), whose frequency in the combined data sets is $P < 10^{-5}$. Color brightness is proportional to the density of overlapping points. Our model, despite its simplicity, explains these patterns.

applicable to most generalized mutualisms. Our simplest model also makes a prediction that is compatible with empirical patterns and in agreement with mounting evidence for the role of weak interactions in community sta-bility (8–12). It remains to be seen whether new models better capture these patterns and improve our understanding of the highly diversified mutualisms among free-living plants, pollina-tors, and seed dispersers.

References and Notes
1. J. Bascompte, P. Jordano, J. M. Olesen, *Science* **312**, 431 (2006).
2. J. N. Holland, T. Okuyama, D. L. DeAngelis, *Science* **313**, 1887 (2006); www.sciencemag.org/cgi/content/full/313/5795/1887b.
3. H. F. Howe, G. F. Estabrook, *Am. Nat.* **111**, 817 (1977).
4. D. Carr, *Can. J. Bot.* **70**, 1784 (1992).
5. R. Sallabanks, *Ecology* **74**, 1326 (1993).
6. J. N. Holland, D. L. DeAngelis, J. L. Bronstein, *Am. Nat.* **159**, 231 (2002).
7. G. Sugihara *et al.*, in *Exploitation of Marine Communities*, R. M. May, Ed. (Springer, Berlin, 1984), pp. 131–153.
8. R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, NJ, 1973).
9. K. McCann, A. Hastings, G. R. Huxel, *Nature* **395**, 794 (1998).
10. G. D. Kokkoris, A. Y. Troumbis, J. H. Lawton, *Ecol. Lett.* **2**, 70 (1999).
11. A.-M. Neutel, J. A. P. Heesterbeek, P. C. Ruiter, *Science* **296**, 1120 (2002).
12. J. Bascompte, C. J. Melián, E. Sala, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 5443 (2005).
13. We thank B. García, L.-F. Bersier, P. Buston, M. A. Fortuna, C. J. Melián, M. Kondoh, G. Sugihara, S. Allesina, and M. Pascual for useful discussions. J. Saldaña and J. L. Garcia-Domingo provided insight into the convergence of the two models. Funding was provided by the Spanish Ministry of Science and Technology (J.B. and P.J.), the Danish Natural Sciences Research Council (to J.M.O.), and the European Heads of Research Councils, the European Science Foundation, and the European Commission Sixth Framework Programme through a EURYI (European Young Investigator) Award (to J.B.).