

## Reply to Kiers et al.: Economic and biological clarity in the theory of mutualism

Kiers et al. (1) make three main points. First, they noted that many mutualisms involve multiple symbionts interacting with a single host. We agree, and we explained that partner fidelity feedback (PFF) can function because plants generally “limit, withdraw, or even abscise investment in shoots, flowers, and roots (or subsets of any of these) after physical damage or deficits of . . . resources. . .” (2). This “modularity” of plant hosts (3) separates the effects of different symbionts and allows the host to react to individual symbionts. Modularity is easily incorporated into our model, because (with no change in our results) principal-agent theory allows the assumption of one agent per host to be replaced with a less restrictive one: let the host react differently to different agents. This assumption is well accepted in plant physiology and by existing mutualism theory (2).

The problem to which we alluded is when hosts cannot react differently, such as when mixtures of symbionts occur within modules. Kiers et al. (1) mention the example of multiple moths on yucca flowers. To the extent that cheater moths individually cause enough damage, cheaters are reliably exposed to host response, but noncheaters escape floral abortion when they do not oviposit alongside cheaters (4).

Second, Kiers et al. (1) state that host response is only “an efficient way of distributing resources to partners differing in net mutualistic benefit, with effects on symbiont fitness as . . . side effects.” Again, we agree. We made the same argument, and dictionary definitions and precedent (2) have led us to call this feedback PFF, whereas Kiers et al. call it host sanction (HS). PFF is the theory that hosts maximize their prospective fitness, e.g., by “balancing the cost of maintaining a damaged. . . part against the cost of abscission and. . . cost of the lost contribution. . . to future growth. . . without. . . consideration of the effect of abscission on [symbiont] fitness. . .” (2). In contrast, under our definition of HS, hosts infer symbiont behavior to punish cheaters, which invokes the game-theoretical concept of commitment.

Regardless of what we call PFF and HS, our contribution was to show how to test for them in real systems. Both require that punishment be sufficiently harmful to the symbiont, so demonstrating that cheaters suffer a fitness-reducing host response is not enough.

Third, Kiers et al. (1) say that our description of the biology of the legume-rhizobia system is incorrect. We strongly disagree. For instance, it is essential to our argument that plants “shut down nodules if they can obtain cheaper N from external sources.” PFF predicts that hosts shut down nodules both when rhizobia cheat and when they get sufficient N from the soil (even though the rhizobia initially continue fixing nitrogen). Similarly, we did not confuse  $N_2$  and  $NH_3$ . The elegant experiment of Kiers et al. (5) made rhizobia “cheat” by exposing roots to an atmosphere lacking  $N_2$ , thereby preventing rhizobia from fixing  $N_2$ . The implicit assumption is that the plants cannot measure  $N_2$  concentration, because if they could, this experiment could be interpreted as indicating how plants respond to a  $N_2$ -poor atmosphere.

We are grateful to Kiers et al. for the opportunity to clarify our arguments.

**E. Glen Weyl<sup>a</sup>, Megan E. Frederickson<sup>b</sup>, Douglas W. Yu<sup>c,d,1</sup>, and Naomi E. Pierce<sup>e</sup>**

<sup>a</sup>Society of Fellows and <sup>c</sup>Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, <sup>e</sup>State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Kunming, Yunnan 650223, China; <sup>d</sup>School of Biological Sciences, University of East Anglia, Norwich, Norfolk NR47TJ UK; and <sup>b</sup>Department of Ecology & Evolutionary Biology, University of Toronto, 25 Harbord Street, Toronto, ON M5S 3G5, Canada

1. Kiers ET, Denison RF, Kawakita A, Herre EA (2011) The biological reality of host sanctions and partner fidelity. *Proc Natl Acad Sci USA* 108:E7.
2. Weyl EG, Frederickson ME, Yu DW, Pierce NE (2010) Economic contract theory tests models of mutualism. *Proc Natl Acad Sci USA* 107:15712–15716.
3. Edwards DP, Hassall M, Sutherland WJ, Yu DW (2006) Selection for protection in an ant-plant mutualism: host sanctions, host modularity, and the principal-agent game. *Proc Biol Sci* 273:595–602.
4. Pellmyr O, Huth CJ (1994) Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* 372:257–260.
5. Kiers ET, Rousseau RA, West SA, Denison RF (2003) Host sanctions and the legume-rhizobium mutualism. *Nature* 425:78–81.

Author contributions: E.G.W., M.E.F., D.W.Y., and N.E.P. wrote the paper.

The authors declare no conflict of interest.

<sup>1</sup>To whom correspondence should be addressed. E-mail: dougwuy@gmail.com.