LETTER

The biological reality of host sanctions and partner fidelity

Weyl et al. (1) used employment contract theory to argue that partner fidelity feedback (PFF) provides a stronger explanation for the evolution of mutualisms than host sanctions (HS). Unfortunately, the article propagates a series of major misunderstandings that require correction.

First, their model assumes a single clone of symbiont per host (1). This fundamental assumption is violated in all mutualisms discussed by Weyl et al. (1) (e.g., figs and wasps, yuccas and moths, legumes and rhizobia, plants and mycorrhizae). Weyl et al. (1) conceded: "the fact that legumes are often infected by multiple strains of rhizobia remains a problem, because our model assumes only one type of agent." This unrealistic assumption is not just a "problem," it is a fatal flaw. Although PFF-type mechanisms can explain cooperation under conditions with one symbiont per host, PFF will break down as symbiont genotype numbers increase (2, and references therein).

Second, Weyl et al. (1) defined sanctions as "the costly, selective punishment of cheating symbionts." This contrasts with previous verbal and mathematical definitions, especially in regards to inherent "costs" (2, 3). It is widely recognized that HS will evolve only if benefits of imposing sanctions outweigh costs to individual hosts (2, 3). Importantly, this net host fitness benefit need not depend on how sanctions affect symbiont evolution, only on how imposing sanctions affects individual host fitness (2, 3). They also incorrectly stated that HS models ". . .emphasize the value of punishment as a public deterrent. . ." This may be true of economic models of human sanctions, but for the plant-based examples cited in the article, sanctions are simply an efficient way of distributing resources to partners differing in net mutualistic benefit, with effects on symbiont fitness as frequent side effects.

Finally, the basic biology is flawed. In their legume–rhizobia example, Weyl et al. (1) incorrectly assumed that rhizobia keep fixing N_2 even upon the addition of nitrate. It is well known that plants will shut down nodules if they can obtain cheaper N from an external sources. Compounding this basic error, Weyl et al. (1) wrote, "Kiers et al. [4] assumed that plants cannot, on a nodule-by-nodule basis, measure the concentration of N_2. . ." Weyl et al. (1) appear to have confused N_2 (substrate, always saturating) with NH_3 (product, which is measured per nodule). In their yucca–yucca moth example, Weyl et al. (1) did not acknowledge that multiple (unrelated) moths lay eggs simultaneously in a single yucca flower [~30% of single flowers have been shown to contain both deep and shallow ovipositions (5)], leading to the erroneous conclusion that the fitness of the host and a single pollinator can be strongly coupled.

Put simply, Weyl et al. (1) have misinterpreted the HS literature, equating sanctions with "costly punishment" that evolves to "discipline" symbiont behavior. They presented a model with unrealistic assumptions, deriving conclusions with little biological relevance. Unfortunately, these fundamental mistakes prevent the article from being a productive mix of economic theory and biology.

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