

# How mutualisms between plants and insects are stabilized

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**While the idea of cooperation between individuals of a species has received considerable attention, how mutualistic interactions between species can be protected from cheating by partners in the interaction has only recently been examined from theoretical and empirical perspectives. This paper is a selective review of the recent literature on host sanctions, partner-fidelity feedback and the concept of punishment in such mutualisms. It describes new ideas, borrowed from microeconomics, such as screening theory with and without competition between potential partners for a host. It explores mutualism-stabilizing mechanisms using examples from interactions between figs and fig wasps, and those between ants and plants. It suggests new avenues for research.**

**Keywords:** Ant–plant interaction, exploitation, fig–fig wasp interaction, mutualism.

Can two walk together, except they be agreed?

Amos 3:3

‘Society may exist among different men, as among different merchants, from a sense of its utility, without any mutual love or affection; and though no man in it should owe any obligation, or be bound in gratitude to any other, it may still be upheld by a mercenary exchange of good offices according to an agreed valuation ... .

... [t]hat action must appear to deserve reward, which appears to be the proper and approved object of that sentiment, which most immediately and directly prompts us to reward, or to do good to another. And in the same manner, that action must appear to deserve punishment, which appears to be the proper and approved object of that sentiment which most immediately and directly prompts us to punish, or to inflict evil upon another.’

Adam Smith, *Theory of Moral Sentiments*, 1759

THE idea of cooperation has long intrigued humans. The early scriptures, and also philosophers such as Thomas Hobbes, author of *Leviathan, or the Matter, Forme, and Power of a Commonwealth, Ecclesiasticall and Civil* (1651) and formulator of social contract theory, as well as

Adam Smith, who is better known as an economist for his treatise titled *An Inquiry into the Nature and Causes of the Wealth of Nations* (1776), wrote about cooperation and the functioning of societies within a utilitarian framework of rewards, services and mutual agreements tempered by punishment. Post-Malthus and Darwin, the idea of relatedness between individuals contributing to cooperation via the process of kin selection and inclusive fitness has also held centre-stage among evolutionary theories<sup>1</sup>, albeit with recent controversies<sup>2,3</sup>. While cooperation between individuals of the same species has received considerable theoretical and empirical consideration particularly within the framework of the prisoner’s dilemma, Tit-for-Tat and other game theoretic formulations<sup>4,5</sup>, the evolution of cooperation between species has received much less attention. However, the last two decades have seen a rapid growth in defining the issues involved in an interspecific mutualistic relationship<sup>6–8</sup>. Understanding the spectacular examples of mutualism seen in nature may be one of the most important challenges for evolutionary biology today.

## When is it co-evolution?

Two-species associations have often been thought of in the context of co-evolution<sup>9</sup>, and co-evolution usually implies an arms race where, like the Red Queen, two partners keep running an evolutionary race to remain in the same relative place<sup>10</sup>. Such arms races are believed to have given rise to the spectacularly long nectar spurs of orchid flowers and the equally long mouthparts or probosces of their pollinating moths<sup>11</sup>. Can such an arms race go on indefinitely? How can co-evolution be stable when two partners may be asymmetrical in their generation times and thereby their per generation mutation rates, as occurs for example in a mutualism between a long-lived tree and a short-lived pollinator? How can mutualisms persist when partners are tempted to cheat, and how might partners prevent or punish cheats or defectors?

In this paper, I will briefly review some recent ideas about how interspecies mutualisms are stabilized, and since the array of such mutualisms is vast, I will focus on two mutualisms with which I have some familiarity, i.e. the mutualism between figs and fig wasps, and that between ants and ant-plants. I will also raise questions

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that remain unresolved in the hope that they will stimulate further research.

Since co-evolution has been such a central idea in the evolution of two-species interactions, it is obvious that the central question to be answered is: When is it co-evolution? This was the title of a short paper written by Daniel Janzen<sup>12</sup> more than 30 years ago; in this paper Janzen raised the possibility that matching traits of two species currently engaged in a mutualism may arise not from co-evolution but from pre-adaptation. According to this idea, a species may have evolved a trait in a different context or in a different geographic location; if this trait now facilitates its association with another species in a new context or in a new geographic location, it may appear to have co-evolved within the existing mutualistic interaction, but the trait is in fact a pre-adaptation. For example, matching between lengths of mouthparts of pollinating moths and those of flower corolla tubes in a particular area may be the result of long-tongued moths with a different evolutionary history migrating from another area and associating with long-tubed flowers in a new location. Obviously, knowledge of the evolutionary history of the partners is crucial in distinguishing between these hypotheses<sup>13</sup>.

### Mutualism-stabilizing mechanisms

A seminal paper to suggest a framework for the examination of interspecies mutualisms was that by James Bull and William Rice<sup>14</sup> in 1991 in which the authors attempted to distinguish one-time interactions from longer term and repeated interactions between individuals of two different species. They introduced the terms partner choice and partner-fidelity feedback, and viewed partner-fidelity feedback as what might occur in an iterated prisoner's dilemma game where the same players encounter each other repeatedly in a series of interactions. They also introduced the idea of 'partner punishment' if expected services were unsatisfactory, and suggested that partner choice, feedback from the interaction and punishment could help to stabilize mutualisms. They viewed partner-fidelity feedback to be relevant in close interactions between hosts and symbionts as might occur especially with vertically transmitted symbionts, whereas partner choice could occur under conditions of horizontal transmission. They also viewed the interaction between the fig and its pollinating fig wasps as one of partner choice.

Critical with regard to mutualism-stabilizing mechanisms are the issues of how the right partners may be recruited, and once an interaction is established, how cheating can be prevented. Using principles borrowed from the economics of incomplete information developed for insurance markets<sup>15</sup>, Archetti and co-workers<sup>16,17</sup> articulated what they call screening theory to suggest how a right partner could be recruited. According to this theory,

the host selects partners by imposing such a level of cost on their symbionts that only certain symbionts with required characteristics will be able to pay this cost; consequently, unsuitable or inappropriate partners automatically get screened out. The following example will clarify this mechanism. A university wants to erect a building to house specialized equipments to be used in specialized research; only certain construction agencies are technically equipped to undertake the construction. The university wants to be very sure that it gets the best pool of applications for this job; it therefore raises the application or contract fee and also advertizes such technical prerequisites that only applicants from this specialized pool can qualify. This is an automatic screening process, and ensures a certain minimum quality of service in the absence of information or with an asymmetry of information, i.e. the contactors have information about their potential client, which is the university in this case, but not vice versa. Why would high quality contractors want to apply only for high quality jobs? This is because the cost of maintaining their specialized construction equipment could only be borne by the acquisition of specialized jobs. According to Archetti *et al.*<sup>16</sup>, in real-life mutualisms, this is how the 'hidden characteristics' problem of the quality of a partner may be solved. This mechanism was also extended to include a competition-based screening wherein hosts may set up a situation by which potential partners are made to compete with each other such that only high quality partners remain in the interaction once they outcompete lower quality interactants<sup>16</sup>.

Once an interaction has been set up, how can the host ensure that the symbiont will not cheat? Can the host impose sanctions on errant symbionts and punish them? There is now considerable theoretical work on the concept of host sanctions<sup>16-19</sup>, and opinions are divided about exactly what the terms used in the literature mean. According to Archetti *et al.*<sup>16</sup>, host sanction refers to a *de novo* adaptation in a host which has arisen in response to the specific act of cheating by a symbiont or partner. Partner-fidelity feedback on the other hand refers to the response of a partner to the outcome of cheating. An example from the plant-insect interaction literature will help to clarify this distinction and to emphasize the importance of recognizing which traits result from pre-adaptation or from co-evolution.

A classic textbook example of a mutualism between plants and their pollinators is that of the yucca and yucca moths<sup>20</sup>. In this mutualism, yucca moth females actively collect pollen using specialized antennal structures and pollinate yucca flowers; they also oviposit into some flower ovules, and their larvae feed on yucca seeds<sup>21</sup>. In a stable relationship between plant and insect, some seeds mature and moth offspring develop from other seed sites. Yucca moth females must pollinate flowers since their larvae depend on seeds as a resource; however, cheating moths may overexploit the yucca flowers by ovipositing

into many ovules. It was found that yuccas abort those fruit which have experienced excessive oviposition<sup>22,23</sup>. The critical issue here is whether this abortion is a specific act of punishment against the act of cheating, i.e. an example of host sanction, or whether it is a general plant response to excessive damage of flowers, or to altered source–sink dynamics where the source is the maternal plant and the sink is constituted by the developing fruit. If the plant is responding to an outcome, i.e. reduced sinks, then partner-fidelity feedback is the likely mechanism. This plant response is likely to be a pre-adaptation to tissue damage or altered source–sink dynamics, which might come about by a variety of abnormal factors such as, poorly developing seeds due to self-pollination or other incompatibilities, or seed damage due to oviposition or other factors. Experiments with ‘artificial’ oviposition using steel pins to mimic the piercing action of moth ovipositors indicated that superficial oviposition did not induce fruit abortion whereas deep oviposition caused fruit drop<sup>24</sup>. It therefore appears that the so-called punishment is actually the outcome of a feedback and that host sanction *per se* has not yet been demonstrated in this system<sup>25</sup>. Most angiosperms appear to employ fruit abortion as a method to effectively allocate resources<sup>26,27</sup>; consequently, these mechanisms have not evolved *de novo* to ‘punish’ cheats.

Another problem, with regard to employing some of the classical game theoretic constructs in plant–insect mutualisms, is the issue of individual recognition. Many games require that individual partners are recognized. It may be possible for insects to recognize certain rewarding or non-rewarding plant individuals by learning their locations<sup>28</sup> or by marking previously visited flowers, and thereby avoiding re-visitation and consequent lower resource acquisition from such resource-depleted flowers<sup>29</sup>. However, it is not yet known whether plants can recognize individual partners, although they may recognize characteristics of individuals or their clones as in rhizobial symbionts within plant roots<sup>30</sup>.

### Stabilizing the fig–fig wasp mutualism

Against this brief backdrop of current theories on conflict resolution, how are mutualisms stabilized in the fig–fig wasp and ant–plant interaction systems? The fig–fig wasp interaction system is a brood site or a seed predation pollination mutualism<sup>31,32</sup>. Here, the fig tree host produces enclosed globular inflorescences called syconia which contain hundreds to thousands of flowers. In typical monoecious figs, syconia are protogynous, maturing the female flowers first. When these flowers are receptive to pollen, the syconium produces volatile signals that attract fig wasp pollinators<sup>33</sup>. These enter the syconium through a single, tight, bract-lined opening called the ostiole, pollinate flowers and also oviposit into some

pollinated flowers before dying within the syconium. Pollinators rarely exit syconia to enter another one for pollination; syconia consequently serve as pollinator traps. Pollinator offspring, however, mature and mate within syconia concordantly with the anthesis of male flowers. Female pollinators exit the syconia laden with pollen from male flowers in search of a pollen-receptive female phase syconium within which they can continue their life cycle. Syconia from which female wasps have exited, and that now contain only lifeless and wingless male wasps, go on to ripen so that the mature fruit containing fully developed seeds may be consumed by seed dispersal agents.

In this system, how do figs prevent cheating pollinators, i.e. those that oviposit excessively within a syconium? Several hypotheses have been posited for the prevention of such acts and thereby the stability of the mutualism. By the unbeatable seeds hypothesis<sup>34</sup>, it was suggested that certain flowers, especially those lining the outermost region of the syconium, are biochemically or physically protected from wasp oviposition, and will always produce only seeds. This hypothesis has never been successfully tested. In the ovipositor length limitation hypothesis, it was suggested that flowers within the syconium vary in style length; consequently the ovules of certain long-styled flowers are out of reach of the pollinator’s ovipositor and cannot be subjected to oviposition<sup>35,36</sup>. From a co-evolutionary perspective, it is possible to envision an arms race between style length and ovipositor length which may be regulated by natural selection against an excessively long and costly ovipositor<sup>35</sup>. Whether this mechanism is in action or not, most ovules in many fig species are reachable by a pollinator’s ovipositor<sup>37</sup>. From the pollinator’s perspective, certain ovules such as the innermost ovules within the syconium lumen may be more profitable<sup>38</sup> or may provide more space for pollinator offspring to grow<sup>39</sup>; these spatial preferences may also preclude excessive and indiscriminate oviposition within the syconium, and thus help to stabilize the mutualism. The fig–fig wasp mutualism is also subject to parasitism by other galling fig wasps, and parasitoids of these parasitic galls as well as of the pollinators. There is now increasing evidence that the presence of these parasites/parasitoids may also help to stabilize the mutualism as they may control the population of pollinators within syconia (A. Krishnan and R. M. Borges, unpublished). Furthermore, pollinators may prefer to exploit the innermost ovules, farthest away from the syconial wall, as this would enable them to escape the reach of the parasitoids’ ovipositors; this preference for oviposition sites so that pollinator offspring develop within enemy-free space has been proposed for some fig systems as a stabilizing mechanism against over exploitation of ovules by the pollinators<sup>40</sup>.

In recent years, Jandér and co-workers have found evidence for abortion of fig syconia in response to excessive

oviposition relative to pollination<sup>41,42</sup>. These authors conducted experiments with pollen-free wasps incapable of causing seed production and compared results with wasps carrying pollen and therefore capable of providing a mutualistic service. They showed that abortion occurred at the level of the syconium and not at the level of the individual exploited flower. While these workers have interpreted their results as deriving from host sanction, it appears that syconium abortion is a generalized response to excessive damage of flowers by oviposition and/or changes in source–sink dynamics. Therefore, a recent review suggests that, as in other angiosperms, and also in the yucca example mentioned earlier, such ‘host sanctions’ are a pre-adapted response to host tissue damage<sup>25</sup> or alteration in source–sink dynamics and not to cheaters *per se*.

In dioecious figs, fig wasps can only breed within syconia on male trees, whereas wasps that enter syconia on female trees are doomed to zero reproductive success since ovules in all flowers within female syconia are out of reach of the female ovipositor; syconia on female trees are therefore ‘tomb blossoms’<sup>31,32</sup>. Furthermore, approximately half of the world’s fig species are dioecious<sup>43</sup>. Why is such a system, in which the plant cheats its partners, stable? Why haven’t wasps evolved to be able to distinguish between male and female trees<sup>44</sup>? Besides other proposed factors, there also appears to be chemical mimicry<sup>45</sup> such that pollinator wasp females are unable to differentiate between the scents of male and female trees (M. Hossaert-McKey and R. M. Borges, unpublished). Is this an evolutionary arms race in action? This is a question that still needs answers.

### Stabilizing ant–plant mutualisms

What about the ant–plant interaction system? How might this system be stabilized against cheaters? Many plants offer rewards to ants in exchange for services<sup>46,47</sup>. Plant rewards are in the form of (a) food for ants which may be extrafloral nectar or solid food bodies rich in lipids and proteins provided from glands on various non-floral plant parts or (b) nesting spaces for ants in the form of swollen structures such as hollow internodes, thorns or tubers. These nesting spaces are referred to as domatia. Rewards provided by ants to their host plants are protection against herbivores, and nitrogen that is absorbed by plants from debris and other ant-derived materials within ant-occupied domatia. While there are many ant-plants and several genera of plant-ants, there are few examples of obligate or specialized mutualists in such interactions. In an Indian ant-plant *Humboldtia brunonis*, the domatia are non-specifically occupied not only by protective and non-protective ants but also by interlopers such as arboreal earthworms<sup>48</sup>; these non-specific domatia occupants contribute to the nitrogen budget of the plant and this is

probably responsible for the maintenance of the domatia trait despite the absence of a protective partner ant across much of this plant’s geographic distribution<sup>49</sup>.

In Mesoamerica, however, there is a high degree of specificity between acacias and *Pseudomyrmex* ants. These acacias provide extrafloral nectar, food bodies and housing to the ants in the form of hollow thorns. Martin Heil and his group have been studying the chemical ecology of this interaction and have found mechanisms by which hosts can screen partners and thereby stabilize mutualisms<sup>50</sup>. In one example, high quality and low quality *Acacia* species occur in sympatry; quality is defined in terms of extrafloral nectar production. Individuals of these species are colonized as saplings by queens of high quality and low quality *Pseudomyrmex* ant species where quality is defined as the ability of the ants to protect their host plant against herbivores. Sometimes high quality and low quality ant queens colonize the same host and set up high and low quality colonies on the same plant. Aggressive high quality colonies outcompete low quality ant species because their defense of plant modules against herbivores leads to better growth of those modules and thereby more production of extrafloral nectar, food bodies and hollow thorns for more nesting spaces, whereas low quality ant species on the same host plant have the opposite effect<sup>51</sup>. Therefore, by competitive feedback processes, high quality ants dominate and take over high quality host plants. This is screening in action as suggested by Archetti and co-workers and is a process which solves the ‘hidden characteristics’ of the partner problem<sup>16</sup>.

Since ant-acacias also provide ants with valuable and nutritious food bodies to nourish their larvae, how do plants prevent the consumption of food bodies by opportunistic, exploitative ants? It is now known that some food bodies contain proteinase inhibitors and only larvae of the mutualistic ant species have proteases that are relatively insensitive to these inhibitors<sup>52</sup>. Larvae of non-adapted ant species, whose digestive enzymes would be inhibited by these compounds, would acquire nutrition at a slower rate; consequently, colonies of such non-adapted ants would grow at slower rates, and thus lose out in a competition with mutualists should mutualistic and non-mutualistic ant species co-colonize the same host. This appears to be a biochemical filter that can prevent undue exploitation of the mutualism. Is this the result of co-evolution or pre-adaptation? Since most plants produce proteinase-inhibitors against insect herbivores, could the resistance to the action of this inhibitor be an example of what has also been described as ecological fitting<sup>53</sup>, i.e. two species jointly being selected for their matching traits, even though such traits have not co-evolved<sup>50</sup>?

Another recently discovered biochemical filter acts on adult ants to ensure the right choice of host plant by the ant. Many ant-acacias produce extrafloral nectar that is sucrose-free, and this has long been described as a specific and unusual property since most ant species can utilize

sucrose by the action of invertase in their guts<sup>54</sup>; indeed, many plant-associated ants also show a preference for sucrose<sup>55</sup> which is commonly present in plant exudates<sup>54</sup>. How then can a sucrose-free extrafloral nectar be explained? Extrafloral nectar is food for adult ants and in some acacias the sucrose-free nectar is also known to contain chitinase which has an inhibitory effect on invertase in the guts of adult mutualistic ants<sup>56</sup>. Therefore, while invertase is active in the guts of ant larvae that are not fed with extrafloral nectar, it is inactivated in the guts of adult ants for whom extrafloral nectar is a major food resource. Lack of functional invertase in the adult ants reinforces their dependency on this peculiar sucrose-free extrafloral nectar, and thereby ensures fidelity of individuals of this particular ant species to their host plants. Such a mechanism is believed to help stabilize the ant-plant relationship.

Ant-plants can also use mechanical filters to keep out parasitic ants as found in the African ant-plant *Leonardoxa* which harbours ants in swollen, hollow stem internodes. The size of the openings of these hollow chambers or domatia vary in different plant populations based on the presence and body size of parasitic ant species, and appears to have evolved to keep the parasitic ants out<sup>57</sup>. The domatia of the Indian ant-plant *H. brunonis*, on the other hand, have large, self-opening slits, which allow the entry of many species of interlopers besides protective ants including ants that castrate host flowers<sup>58</sup>. As mentioned earlier, perhaps there is less selection on the plant to restrict entrants into the domatia because of the nitrogen benefits accruing to the plants from the interloping inhabitants such as earthworms<sup>49</sup>.

### Red Queen, Red Kings, and the 'individual' plant

At the beginning of this paper, the following question was posed: How might co-evolution actually occur if host and symbiont have different generation times? How might long-lived trees with long generation times keep up in a co-evolutionary battle against short-lived exploiters of mutualisms such as cheating wasps and ants? Some modelling efforts have suggested a Red King effect in which the slowest evolving partner wins the evolutionary race<sup>59,60</sup>. However, there may be problems with the existing formulation of this effect in realistic situations which involve multiple players (individuals) rather than two-player situations<sup>61,62</sup>. How else might evolutionary rates match? There is evidence for somatic genetic mutations in plants at the level of new meristems and possible intraorganismal selection of suitable meristems<sup>63,64</sup>. There are viewpoints that call into question previous definitions of plant individuality, that suggest that individual plants should be considered as metapopulations, and that advocate that plant modules could also be individuals if they have arisen from mutated meristems, giving rise to

gametes that would necessarily be different from those of the 'original' individual<sup>65,66</sup>. If this is a tenable perspective, it is then possible to imagine a long-lived tree being made up of many independent genetic units. Could this phenomenon help to overcome the problem of asymmetry in co-evolutionary rates between partners? Individual strangler figs can consist of multiple genotypes<sup>67</sup>, and this phenomenon was explained by a coalescence of the somatic tissue of seedlings germinating in close proximity to form chimeric individuals. In figs, as pointed out earlier, 'sanctions' against excessive abortion occur at the level of the syconium, not at the flower or the whole plant level. The syconia in different parts of the plant arise from different meristems and therefore are borne on different modules. In ant-plants, exploiters that inhabit domatia may parasitise certain modules of the plant, and since the photosynthetic resources to nourish a domatium come from tissue and leaves subtended by the module of which the domatium is the unit, any action by the ant that reduces the efficiency of resource garnering by the module (e.g. herbivory which reduces photosynthetic area) will feedback negatively on the ant colony itself<sup>68</sup>. Similarly, any mutation in a meristem resulting in modules which produce superior resources for ants may be effectively selected for within the ant-plant by feedback processes from the ants. Thus, it appears that multiple games could be played at the level of intraplant modules in the interactions between plants and insects.

While evolutionary theory has helped to clarify the distinctions between phenomena that are evident in plant-insect interactions, it still lacks good formulation of multiplayer games<sup>66</sup> which are required for understanding mutualisms in the real world. It also lacks models that can incorporate the newer perspectives on plant modularity and individuality, although there are recent efforts in this direction for antagonistic interactions between plants and insects in the context of herbivory<sup>69</sup>. The field of mutualism also greatly lacks good empirical data on mechanisms involved in partner choice, host sanctions, and other measures by which mutualisms can be stabilized and protected from exploitation. While an earlier review exhorted modellers to come up with suitable models for mutualism<sup>6</sup>, the newer call is also for better data to demonstrate what theory suggests<sup>25,70</sup>. The field is wide open for investigation.

1. Hamilton, W. D., The genetical evolution of social behaviour, I, II. *J. Theor. Biol.*, 1964, **7**, 1–16.
2. Nowak, M. A., Tarnita, C. E. and Wilson, E. O., The evolution of eusociality. *Nature*, 2006, **466**, 1057–1062.
3. Abbot, P. *et al.*, Inclusive fitness theory and eusociality. *Nature*, 2011, **466**, 1057–1062.
4. Maynard Smith, J., *Evolution and the Theory of Games*, Cambridge University Press, 1982.
5. Sigmund, K., *Games of Life*, Penguin, London, 1995.
6. Bshary, R. and Bronstein, J., Game structures in mutualistic interactions: what can the evidence tell us about the kinds of models we need? *Adv. Study Behav.*, 2004, **34**, 59–101.

7. Sachs, J. L., Mueller, U. G., Wilcox, T. P. and Bull J. J., The evolution of cooperation. *Q. Rev. Biol.*, 2004, **79**, 135–160.
8. Leigh Jr, E. G., The evolution of mutualism. *J. Evol. Biol.*, 2010, **23**, 2507–2528.
9. Thompson, J. N., *The Coevolutionary Process*, University of Chicago Press, 1994.
10. Van Valen, L., A new evolutionary law. *Evol. Theor.*, 1973, **1**, 1–30.
11. Nilsson, L. A., Deep flowers for long tongues. *Trends Ecol. Evol.*, 1998, **13**, 259–260.
12. Janzen, D. H., When is it coevolution? *Evolution*, 1980, **34**, 611–612.
13. Whittall, J. B. and Hodges, S. A., Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature*, 2007, **447**, 706–709.
14. Bull, J. J. and Rice, W. R., Distinguishing mechanisms for the evolution of co-operation. *J. Theor. Biol.*, 1991, **149**, 63–74.
15. Rothschild, M. and Stiglitz, J. E., Equilibrium in competitive insurance markets: an essay on the economics of imperfect information. *Q. J. Econ.*, 1976, **90**, 626–649.
16. Archetti, M., Scheuring, I., Hoffman, M., Frederickson, M. E., Pierce, N. E. and Yu, D. W., Economic game theory for mutualism and cooperation. *Ecol. Lett.*, 2011, **14**, 1300–1312.
17. Archetti, M., Úbeda, F., Fudenberg, D., Green, J., Pierce, N. E. and Yu, D. W., Let the right one in: a microeconomic approach to partner choice in mutualisms. *Am. Nat.*, 2011, **177**, 75–85.
18. Weyl, E. G., Frederickson, M. E., Yu, D. W. and Pierce, N. E., Economic contract theory test models of mutualism. *Proc. Natl. Acad. Sci., USA*, 2010, **107**, 15712–15716.
19. Archetti, M., Contract theory for the evolution of cooperation: the right incentives attract the right partners. *J. Theor. Biol.*, 2011, **269**, 201–207.
20. Pellmyr, O. and Leebens-Mack, J., Forty million years of mutualism: evidence for Eocene origin of the yucca–yucca moth association. *Proc. Natl. Acad. Sci. USA*, 1999, **96**, 9178–9183.
21. Pellmyr, O. and Krenn, H. W., Origin of a complex key innovation in an obligate insect–plant mutualism. *Proc. Natl. Acad. Sci., USA*, 2002, **99**, 5498–5502.
22. Pellmyr, O. and Huth, C. J., Evolutionary stability of mutualism between yuccas and yucca moths. *Nature*, 1994, **372**, 257–260.
23. Pellmyr, O. and Huth, C. J., Reply to Richter and Weiss. *Nature*, 1995, **376**, 558.
24. Marr, D. L. and Pellmyr, O., Effect of pollinator-inflicted ovule damage on floral abscission in the yucca–yucca moth mutualism: the role of mechanical and chemical factors. *Oecologia*, 2003, **136**, 236–243.
25. Frederickson, M. E., Rethinking mutualism stability: cheaters and the evolution of sanctions. *Q. Rev. Biol.*, 2013, **88**, 269–295.
26. Stephenson, A. G., Flower and fruit abortion: proximate causes and ultimate functions. *Annu. Rev. Ecol. Syst.*, 1981, **12**, 253–279.
27. Meyer, K. M., Soldaat, L. L., Auge, H. and Thulke, H.-H., Adaptive and selective seed abortion reveals complex conditional decision making in plants. *Am. Nat.*, 2014, **183**, 376–383.
28. Lihoreau, M., Chittka, L. and Raine, N. E., Trade-off between travel distance and prioritization of high-reward sites in traplining bumblebees. *Func. Ecol.*, 2011, **25**, 1284–1292.
29. Saleh, N., Ohashi, K., Thomson, J. D. and Chittka, L., Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers. *Anim. Behav.*, 2006, **71**, 847–854.
30. Cullimore, J. V., Ranjeva, R. and Bono, J. J., Perception of lipochitooligosaccharidic Nod factors in legumes. *Trends Plant Sci.*, 2001, **6**, 24–30.
31. Cook, J. M. and Rasplus, J.-Y., Mutualists with attitude: coevolving fig wasps and figs. *Trends Ecol. Evol.*, 2003, **18**, 241–248.
32. Herre, E. A., Jandér, K. C. and Machado, C. A., Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annu. Rev. Ecol. Evol. Syst.*, 2008, **39**, 439–458.
33. Grison-Pigé, L., Bessièrre, J.-M. and Hossaert-McKey, M., Specific attraction of fig-pollinating wasps: role of volatile compounds released by tropical figs. *J. Chem. Ecol.*, 2002, **28**, 283–295.
34. West, S. A. and Herre, E. A., The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. *Proc. R. Soc. Lond. B*, 1994, **258**, 67–72.
35. Ganeshaiah, K. N., Kathuria, P., Uma Shaanker, R. and Vasudeva, R., Evolution of style-length variability in figs and optimization of ovipositor length in their pollinator wasps: a coevolutionary model. *J. Genet.*, 1995, **74**, 25–39.
36. Kathuria, P., Ganeshaiah, K. N., Uma Shaanker, R. and Vasudeva, R., Is there dimorphism for style lengths in monoecious figs? *Curr. Sci.*, 1995, **68**, 1047–1049.
37. Ghara, M., Ranganathan, Y., Krishnan, A., Gowda, V. and Borges, R. M., Divvyng up an incubator: how parasitic and mutualistic fig wasps use space within their nursery microcosm. *Arthropod-Plant Interact.*, 2014, **8**, 191–203.
38. Yu, D. W. *et al.*, Oviposition strategies, host coercion and the stable exploitation of figs by wasps. *Proc. R. Soc. Lond. B*, 2004, **271**, 1185–1195.
39. Anstett, M.-C., Unbeatable strategy, constraint and coevolution, or how to resolve evolutionary conflicts: the case of the fig/wasp mutualism. *Oikos*, 2001, **95**, 476–484.
40. Dunn, D. W., Segar, S. T., Ridley, J., Chan, R., Crozier, R. H., Douglas, W. Y. and Cook, J. M., A role for parasites in stabilising the fig–pollinator mutualism. *PLoS Biol.*, 2008, **6**, e59.
41. Jandér, K. C. and Herre, E. A., Host sanctions and pollinator cheating in the fig tree–fig wasp mutualism. *Proc. R. Soc. Lond. B*, 2010, **277**, 1481–1488.
42. Jandér, K. C., Herre, E. A. and Simms, E. L., Precision of host sanctions in the fig tree–fig wasp mutualism: consequences for uncooperative symbionts. *Ecol. Lett.*, 2012, **15**, 1362–1369.
43. Harrison, R. D. and Yamamura, N., A few more hypotheses for the evolution of dioecy in figs (*Ficus*, Moraceae). *Oikos*, 2003, **100**, 628–635.
44. Patel, A., Anstett, M.-C., Hossaert-McKey, M. and Kjellberg, F., Pollinators entering female dioecious figs: why commit suicide? *J. Evol. Biol.*, 1995, **8**, 301–313.
45. Soler, C. C., Proffit, M., Bessièrre, J.-M., Hossaert-McKey, M. and Schatz, B., Evidence for intersexual chemical mimicry in a dioecious plant. *Ecol. Lett.*, 2012, **15**, 978–985.
46. Heil, M. and McKey, D., Protective ant–plant interactions as model systems in ecological and evolutionary research. *Annu. Rev. Ecol. Evol. Syst.*, 2003, **34**, 425–453.
47. Mayer, V. E., Frederickson, M. E., McKey, D. and Blatrix, R., Current issues in the evolutionary ecology of ant–plant symbioses. *New Phytol.*, 2014, **202**, 749–764.
48. Gaume, L., Shenoy, M., Zacharias, M. and Borges, R. M., Coexistence of ants and an arboreal earthworm in a myrmecophyte of the Indian Western Ghats: anti-predation effect of the earthworm mucus. *J. Trop. Ecol.*, 2006, **22**, 341–344.
49. Chanam, J., Sheshshayee, M. S., Kasinathan, S., Jagdeesh, A., Joshi, K. A. and Borges, R. M., Nutritional benefits from domatia inhabitants in an ant–plant interaction: interlopers do pay the rent. *Func. Ecol.*, 2014, **28**, 1107–1116.
50. Orona-Tamayo, D. and Heil, M., Stabilizing mutualisms threatened by exploiters: new insights from ant–plant research. *Biotropica*, 2013, **45**, 654–665.
51. Heil, M., Let the best one stay: screening of ant defenders by *Acacia* host plants function independently of partner choice or host sanctions. *J. Ecol.*, 2013, **101**, 684–688.
52. Orona-Tamayo, D., Wielsch, N., Blanco-Labra, A., Svatos, A., Farías-Rodríguez, R. and Heil, M., Exclusive rewards in mutualisms: ant proteases and plant protease inhibitors create a lock–key

- system to protect *Acacia* food bodies from exploitation. *Mol. Ecol.*, 2013, **22**, 4087–4100.
53. Janzen, D. H., On ecological fitting. *Oikos*, 1985, **45**, 308–310.
  54. Heil, M., Büchler, R. and Boland, W., Quantification of invertase activity in ants under field conditions. *J. Chem. Ecol.*, 2005, **31**, 431–437.
  55. Blüthgen, N. and Fiedler, K., Preferences for sugars and amino acids and their conditionality in a diverse nectar-feeding ant community. *J. Anim. Ecol.*, 2004, **73**, 155–166.
  56. Heil, M., Barajas-Barron, A., Orona-Tamayo, D., Wielsch, N. and Svatos, A., Partner manipulation stabilises a horizontally transmitted mutualism. *Ecol. Lett.*, 2014, **17**, 185–192.
  57. Brouat, C., Garcia, N., Andary, C. and McKey, D., Plant lock and ant key: pairwise coevolution of an exclusion filter in an ant–plant mutualism. *Proc. R. Soc. Lond. B*, 2001, **268**, 2131–2141.
  58. Shenoy, M. and Borges, R. M., Geographical variation in an ant–plant interaction correlates with domatia occupancy, local ant diversity, and interlopers. *Biol. J. Linn. Soc.*, 2010, **100**, 538–551.
  59. Bergstrom, C. T. and Lachmann, M., The Red King effect: when the slowest runner wins the coevolutionary race. *Proc. Natl. Acad. Sci., USA*, 2003, **100**, 593–598.
  60. Bergstrom, C. T. and Lachmann, M., The Red King effect: evolutionary rates and the division of surpluses in mutualisms. In *Genetics and Cultural Evolution of Cooperation* (ed. Hammerstein, P.), MIT Press, 2003, pp. 223–238.
  61. Gokhale, C. S. and Traulsen, A., Mutualism and evolutionary multiplayer games: revisiting the Red King. *Proc. R. Soc. Lond. B*, 2012, **279**, 4611–4616.
  62. Gokhale, C. S. and Traulsen, A., Evolutionary multiplayer games. *Dyn. Games Appl.*, 2014, **4**, 468–488.
  63. White, J., The plant as a metapopulation. *Annu. Rev. Ecol. Syst.*, 1979, **10**, 109–145.
  64. Whitham, T. G. and Slobodchikoff, C. N., Evolution by individuals, plant–herbivore interactions and mosaics of genetic variability: the adaptive significance of somatic mutations in plants. *Oecologia*, 1981, **49**, 287–292.
  65. Clarke, E., Plant individuality and multilevel selection theory. In *Major Transitions in Evolution Revisited* (eds Sterelny, K. and Calcott, B.), MIT Press, Cambridge, 2010, pp. 227–251.
  66. Clarke, E., Plant individuality: a solution to the demographer’s dilemma. *Biol. Philos.*, 2012, **27**, 321–361.
  67. Thomson, J. D., Herre, E. A., Hamrick, J. L. and Stone, J. L., Genetic mosaics in strangler fig tree: implications for tropical conservation. *Science*, 1991, **254**, 1214–1216.
  68. Edwards, D. P., Hassall, M., Sutherland, W. J. and Yu, D. W., Selection for protection in an ant–plant mutualism: host sanctions, host modularity, and the principal-agent game. *Proc. R. Soc. Lond. B*, 2006, **273**, 595–602.
  69. Folse III, H. J. and Roughgarden, J., Direct benefits of genetic mosaicism and intraorganismal selection: modelling coevolution between a long-lived tree and a short-lived herbivore. *Evolution*, 2011, **66**, 1091–1113.
  70. Bronstein, J. L., Proteases hold the key to an exclusive mutualism. *Mol. Ecol.*, 2014, **22**, 3882–3884.

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