Article (refereed)

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6 # Tolerance traits and the stability of mutualism

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1   **Abstract**

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4   Identifying factors which allow the evolution and persistence of cooperative

5   interactions between species is a fundamental issue in evolutionary ecology. Various

6   hypotheses have been suggested which generally focus on mechanisms that allow

7   cooperative genotypes in different species to maintain interactions over space and

8   time. Here, we emphasise the fact that even within mutualisms (interactions with net

9   positive fitness effects for both partners), there may still be inherent costs, such as the

10   occasional predation by ants upon aphids. Individuals engaged in mutualisms benefit

11   from minimising these costs as long as it is not at the expense of breaking the

12   interspecific interaction, which offers a net positive benefit. The most common and

13   obvious defence traits to minimise interspecific interaction costs are resistance traits,

14   which act to reduce encounter rate between two organisms. Tolerance traits, in

15   contrast, minimise fitness costs to the actor, but without reducing encounter rate.

16   Given that, by definition, it is beneficial to remain in mutualistic interactions, the only

17   viable traits to minimise costs are tolerance-based 'defence' strategies. Thus, we

18   propose that tolerance traits are an important factor promoting stability in mutualisms.

19   Furthermore, because resistance traits tend to propagate coevolutionary arms races

20   between antagonists, whilst tolerance traits do not, we also suggest that tolerance-

21   based defence strategies may be important in facilitating the transition from

22   antagonistic interactions into mutualisms. For example, the mutualism between ants

23   and aphids has been suggested to have evolved from parasitism. We describe how

24   phenotypic plasticity in honeydew production may be a tolerance trait that has

25   prevented escalation into an antagonistic arms race and instead led to mutualistic

26   coevolution.

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1   Introduction

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3   Mutualisms are best conceptualised as reciprocally exploitative relationships

4   (Thompson 1982, Janzen 1985, Bronstein 1994, Herre, Knowlton and Mueller 1999)

5   and, rather than viewing mutualism and antagonism as separate fields of study, much

6   can be gained from drawing parallels between the two and identifying fundamental

7   coevolutionary processes that govern both types of interaction. Although mutualisms

8   are defined as net positive interactions for both partners, they often comprise both

9   positive and negative interaction components (van Baalen and Jansen 2001, Bruno,

10   Stachowicz and Bertness 2003). Organisms benefit from maximising positive

11   components towards themselves, even if this is at the expense of costs to the partner.

12   Thus conflict often occurs within mutualisms, where cheats arise and try to obtain

13   benefits from a partner, yet offer nothing in return, thereby making the interactions

14   unstable (the problem of the successful 'defect' strategy in the Prisoner's Dilemma

15   game) (Axelrod and Hamilton 1981). These cheats are less apparent in pure 'by-

16   product mutualisms' *sensu* Connor (1995),where partners simply trade unwanted

17   waste products or cheap services (e.g. Matsuda and Shimada 1993); but cheats are

18   most problematic in 'investment mutualisms' where partners pay a cost for the

19   interaction, and this cost can be reneged upon by cheats (e.g. Yu and Pierce 1998).

20   In this essay, we present an additional hypothesis for the formation and stability of

21   mutualisms based on the type of defence trait used by species to cope with the costs of

22   the interaction. We propose that tolerance traits, rather than resistance traits, facilitate

23   the formation of proto-mutualistic interactions. Futhermore, tolerance traits promote

24   stability in these interactions, thereby paving the way for further mutualistic

25   coevolution. Interactions between ants and mutualistic aphids may be an example of

26   how tolerance traits have been important in the development and maintenance of

27   stability in mutualisms.

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Definitions

The distinction between tolerance and resistance traits was first recognised in plant-herbivore interactions (Painter 1958, Rausher and Simms 1989, Fineblum and Rausher 1995, Strauss and Agrawal 1999). To cope with herbivory, resistance traits (e.g. thorns, trichomes, leaf tannins) minimise the damage a plant experiences (Rausher and Simms 1989) while tolerance traits (e.g. plant compensatory growth in response to herbivory) reduce the fitness consequences of any damage caused (Painter 1958). More specifically, tolerance has been defined as the slope of a regression of fitness on damage for a group of related individuals (Mauricio, Rausher and Burdick 1997, Strauss and Agrawal 1999). In this context, resistance would be the ability to reduce damage and shift any given interaction towards the y-intercept (zero damage). Rather than being solely restricted to plant- herbivore interactions, however, resistance and tolerance traits are also apparent in other antagonistic relationships, such as interactions between hosts and parasites (Roy and Kirchner 2000, Koskela, Puustinen, Salonen and Mutikainen 2002, Miller, White and Boots 2006, Råberg, Sim and Read 2007).

Whilst damage to plants by herbivores can be reasonably assessed by measuring tissue loss, however, the damage caused to hosts by parasites (i.e. internal disruption of vital host processes) is less easy to measure directly. Surrogates for damage, such as parasite burden, can by used, but there is no guarantee that parasite load is directly proportional to the damage done by them. The only way to accurately measure damage to hosts is with recourse to host fitness loss. However, defining damage through fitness loss and then defining tolerance as the slope of damage on fitness is clearly not sensible. Roy and Kirchner (2000) instead define resistance in host-parasite interactions as traits that prevent infection or limit its extent, while tolerance traits do not reduce or eliminate infection but instead offset or reduce its fitness consequences. This definition of tolerance focuses on the reduction or elimination of the antagonist, rather than on 'damage' to the host. Indeed, by Roy and Kirchner's (2000) definition of tolerance, it is conceivable that damage to hosts could be reduced (the definition of a resistance trait in plants), yet the trait would still be classified as tolerance as long as infection levels by parasites were not reduced. Roy and Kirchner's (2000) definition is also very specific to host- parasite interactions, however, and cannot be applied to plants and herbivores. We propose more general

1 definitions of resistance and tolerance, which encompass all antagonistic interactions

2 (see Box 1). In general, resistance traits limit fitness loss to an actor through reducing

3 encounters with the antagonist. Tolerance traits limit fitness loss to an actor without

4 reducing encounters with the antagonist.

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6 **Box 1**

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8 RESISTANCE

9 **Resistance traits limit fitness loss by reducing encounters with an antagonist.**

10 This is achieved in one of four ways. The first three mechanisms are often regarded as

11 'qualitative resistance', whilst the last as 'quantitative resistance':

12 **Evasion**- traits that move the organism away from its antagonist (e.g. good hearing,

13 smell, vision and cooperative alarm behaviours to detect predators, along with

14 morphological and behavioural adaptations to escape them).

15 **Deterrence**- traits that force the antagonist to move away from the actor (e.g. the

16 odorous secretions of skunks; toxic secondary chemicals, thorns and trichomes in

17 plants).

18 **Exclusion**- traits that simply maintain an impermeable barrier between actor and

19 antagonist (e.g intricate floral structures preventing nectar thieves; narrow ostioles of

20 figs preventing seed parasites).

21 **Elimination/ antibiosis**- traits that destroy or harm the antagonist by limiting or

22 reducing its growth rate, thereby reducing encounter between actor and antagonist.

23 (e.g. lymphocyte cells in the immune system that target pathogenic bacteria; plant

24 secondary chemicals which adversely affect insect herbivores [*]).

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26 TOLERANCE

27 **Tolerance traits minimise fitness loss to the actor but without reducing**

28 **encounter rate.**

29 Several different categories of tolerance can be identified:

30 **Compensation-** A given level of herbivory causes less fitness loss to plants because

31 of efficient tissue regrowth.

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[*] Natural selection or learning may convert antibiosis traits into deterrence if the insect begins to avoid the plant (antixenosis).

1 **Bribes-** Attacks from antagonists are reduced through the host/ prey offering

2 alternative goods or services (e.g. production of high quality honeydew by aphids to

3 divert ant predation).

4 **Antidotes-** Antagonists may cause incidental damage to hosts that is not adaptive (i.e.

5 the damage is not correlated with increased fitness of the antagonist). In this case,

6 hosts can evolve 'antidote' traits that reduce consequences of damage without

7 necessarily reducing antagonist fitness (e.g antibody-mediated neutralisation of toxins

8 in mammals).

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10 **Tolerance traits increase the probability of transition into mutualism**

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12 We suggest that the type of defence strategy used by an actor may affect the

13 probability of antagonistic interactions switching to mutualism. Resistance and

14 tolerance traits have different effects on the encounter rate between actors and

15 antagonists, and this will result in different implications for the fitness of antagonist

16 individuals (Roy and Kirchner 2000, Tiffin 2000, Miller and Boots 2005). Reduced

17 encounter rates, achieved through resistance traits, make actors less available for

18 antagonists, therefore antagonist fitness is often reduced (Strauss and Agrawal 1999).

19 This leads to increased selection pressure on antagonists to locate and encounter

20 actors and may also increase virulence. Thus, resistance traits can lead to

21 coevolutionary arms races (Clayton, Lee, Tompkins and Brodie 1999, Strauss and

22 Agrawal 1999, Juenger and Lennartsson 2000, Rausher 2001).

23   Tolerance traits, in contrast, do not reduce the encounter rate between actor and

24 antagonist. Their fitness effects on antagonists are often neutral (Rosenthal and

25 Kotanen 1994, Strauss and Agrawal 1999, Juenger and Lennartsson 2000, Tiffin

26 2000), so they do not trigger coevolutionary arms races, which are unlikely to favour

27 the development of mutualism. Furthermore, sometimes tolerance traits may even

28 have positive fitness effects on antagonists, increasing encounter rate, and leading to

29 more stable and persistent interactions (Roy and Kirchner 2000). For example,

30 herbivores may have increased performance when feeding on higher nutritive value

31 regrowth tissue (Stinchcombe 2002). Such, increased interaction between two groups

32 of organisms may increase the chances of a shift towards mutualism. Indeed,

33 theoretical models predicting the requisite conditions for the evolution of mutualism

1 often identify the frequency of establishment of interactions (encounter rate) between

2 individuals as an important factor (e.g. Roughgarden 1975, Keeler 1981).

3   If tolerance defence strategies do indeed increase the probablility of transition into

4 mutualism, then it is fitting to ask what factors lead to the adoption of tolerance, rather

5 than resistance, traits? It should be noted at this point that defence strategies need not

6 be dichotomous, based solely on tolerance or resistance. Rather these two strategies

7 form the extremes of a continuum. Actual defence strategies may be mixed, involving

8 several different tolerance and resistance traits. For example, the human immune

9 system comprises resistance traits such as oily skin to exclude pathogens and T-killer

10 cells to destroy invaders, but also tolerance traits in the form of antibody-producing B

11 cells that neutralise antigens but do not reduce pathogen load. Trees with modular

12 construction may also evolve a mosaic of shifting resistance-tolerance to enable

13 different parts of their canopy to endure more or less herbivory in turn (Leather 2000).

14 Whereabouts a lineage's defence strategy lies on the resistance- tolerance continuum

15 is likely to determine the chances of an antagonistic relationship de-escalating into a

16 mutually beneficial one. Further study is warranted in this area, although one possible

17 factor affecting type of defence strategy could be the allocation cost of mounting

18 tolerance or resistance traits. The shape of the curve describing the relationship

19 between resource cost and amount of resistance or tolerance gained is likely to affect

20 the evolution of these traits. Another factor affecting the type of defence strategy is

21 the intensity of the cost on the actor imposed by the antagonist (Restif and Koella

22 2004). Very costly, or virulent, antagonists are more likely to select for resistance

23 traits. For example, predators that kill their prey exact the maximum possible cost,

24 and it is hard to tolerate being eaten (Dawkins and Krebs 1979)! Conversely, as costs

25 from the interaction decrease, then selection can favour more tolerance based defence

26 traits. Finally, in mutualistic interactions between co-operator genotypes resistance

27 traits become maladaptive and tolerance traits are the only viable defence strategy.

28 Thus, as the cost-benefit ratio changes, so does the optimum defence strategy (Fig. 1).

29   We should clarify here that by 'mutualistic interaction' we refer specifically to

30 reciprocally beneficial interactions between co-operating genotypes. These

31 interactions form the basis for 'mutualism' between two species. Mutualisms,

32 however, are often parasitized by cheats that threaten the stability of the positive

33 interactions between species. We define the interaction between an individual of one

34 species and a cheating genotype from the second species as an antagonistic

interaction, as there are net fitness costs upon the individual of the first species. Thus, mutualisms between species contain mainly mutualistic interactions with cooperators but also antagonistic interactions with cheats. Much previous theory has concentrated on mechanisms by which cooperators of different species maintain coupling through time (e.g. partner choice (Nilson 1988, Bull and Rice 1991, Broughton, Jabbouri and Perret 2000, Brouat, Garcia, Andary and McKey 2001), and partner fidelity (Bull and Rice 1991, Margulis and Fester 1991, Herre 1993, Herre, Knowlton and Mueller 1999, Bot, Rehner and Boomsma 2001, Thompson 2005)) and by which antagonistic interactions with cheats are limited (e.g. host sanctions and punishment (Trivers 1971, Axelrod and Hamilton 1981, Pellmyr and Huth 1994, Johnstone and Bshary 2002, Hoeksema and Kummel 2003, Kiers, Rousseau, West and Denison 2003, Bshary and Grutter 2005, Edwards, Hassall, Sutherland and Yu 2006)). These mechanisms are highly important in preventing the breakdown of mutualisms. We suggest, however, that in addition to these mechanisms tolerance traits may be crucial in a) the formation of new mutualisms and, b) maintenance of stability in existing mutualisms by limiting any costs imposed by cooperative genotypes, yet while maintaining a net positive interaction. Thus, within a mutualism tolerance traits may be directed towards cooperative genotypes, whilst resistance traits are simultaneously directed towards cheats.
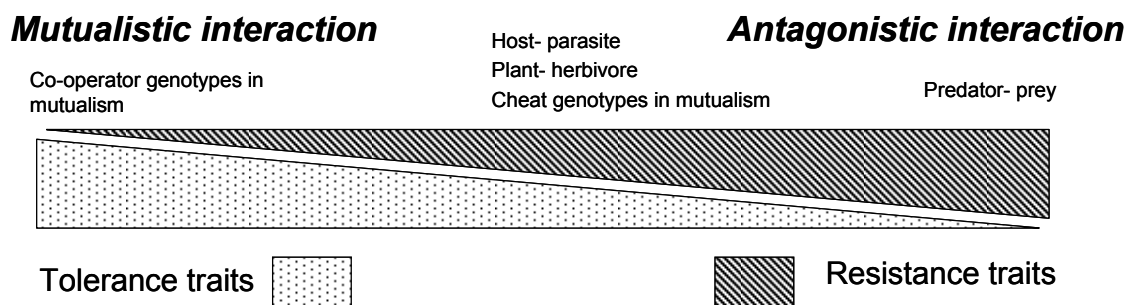
Mutualistic interaction   Host- parasite   **Antagonistic interaction**
                                            Plant- herbivore
Co-operator genotypes in   Cheat genotypes in mutualism   Predator- prey
mutualism

Tolerance traits   Resistance traits

Fig. 1, As the total interaction cost for the actor increases (from mutualism through to weak and then virulent antagonism), there is increased selection to adopt resistance defence strategies. For predator prey interactions, resistance traits are the only option. Weakly antagonistic interactions may result in both types of defence trait, while for mutualistic interactions, tolerance traits are the only viable defence strategy.

1 **Tolerance traits increase the stability of mutualisms**

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3 Reciprocal positive interactions between species are often transient because there is

4 no co-adaptation that couples species in space and time. Similarly, interactions

5 between species may sometimes be mutually beneficial under certain circumstances

6 yet not under others (e.g. parasitic bacteriophages conferring antibiotic resistance to

7 bacteria may be beneficial in growth media containing antibiotics (Normark and

8 Normark 2002)).

9 When mutually beneficial interactions are sufficiently stable (lineages of either

10 species are repeatedly in contact over adequate evolutionary time), then adaptations

11 can arise that faciliate the interaction by increasing the frequency, or maintaining the

12 duration of, interspecific encounters. Such mutualistic coevolution increases mutual

13 benefits, but also increases reliance on the partner, as adaptations for mutualism often

14 have allocation costs (Connor 1995), and can reduce the fitness of mutualistic

15 genotypes in environments where the partner is absent (De Mazancourt, Loreau and

16 Dieckmann 2005). Mutualistic coevolution is thus a positive feedback process,

17 increasing stablility in the interactions between species. The results are the highly

18 coevolved interactions that are used as textbook examples of mutualisms between

19 species, such as the pollination of fig trees by highly adapted agaonid wasps (Janzen

20 1979, Weiblen 2002, Cook and Rasplus 2003). What factors, however, allow transient

21 positive interactions to begin this gradual process of coevolution?

22 We propose that the type of defence strategy used by a species may be very

23 important in increasing the stability of positive interactions. The consideration of

24 defence strategies for the formation and stability of mutualisms is relevant because

25 many mutualisms have arisen from previously antagonistic interactions (Thompson

26 1982, Price 1997, Saikkonen, Faeth, Helander and Sullivan 1998, Jousselin, Rasplus

27 and Kjellberg 2001, Westerbergh 2004). Also, as mentioned earlier, even highly

28 coevolved mutualistic interactions have inherent costs that can be minimised using

29 defences. Proximate mutualisms, in which removal of each partner results in a

30 decreased performance of the other (sensu De Mazancourt, Loreau and Dieckmann

31 2005), can arise from antagonistic interactions through evolved dependence (e.g.

32 amoeba becoming dependent on parasitic bacteria for their functioning (Jeon 1972)),

33 or through context dependence, such as in antibiotic resistance-conferring phages and

34 bacteria (Normark and Normark 2002). When these proximate mutualisms occur,

resistance traits become maladaptive, because they reduce encounter rate with the partner species. Any kind of evasion, deterrence, elimination or exclusion of the partner will reduce fitness of the actor, because the interaction is mutualistic and reducing encounter with a mutualist is, by definition, maladaptive. Instead, tolerance traits will be selected for to cope with any costs inherent in the interaction. Tolerance traits minimise fitness costs to the actor, but they do so without reducing encounter rate, and so without sacrificing the overall benefits achieved from the interaction. This adoption of tolerance traits rather than resistance reduces the 'pulling apart' of the focal species, i.e. it reduces the evolution of traits that create asynchrony in space and time between the two species. Instead, synchrony is reinforced and the stability of the mutualistic interaction is promoted. Furthermore, whereas resistance traits reduce the fitness of the second species, potentially leading to antagonistic coevolutionary arms races, tolerance traits may have neutral or positive fitness effects.

We must stress that this view of the importance of tolerance traits in the stability of mutualistic interactions is very provisional and would certainly benefit from further investigation, such as the quantitative models used to test previous mutualism theory (e.g. see Hoeksema and Bruna 2000 for a review). In the next paragraph, we offer an example of how tolerance traits may partially explain a well known mutualism.

Ants and aphids- an example of tolerance traits facilitating a mutualism?

Ants (Hymenoptera: Formicidae) and aphids (Hemiptera: Sternorrhyncha: Aphidoidea) present an interesting system to consider the emergence of resistance and tolerance traits. Ants often tend aphids for honeydew, which they use as a fuel for foraging, but sometimes also prey upon aphids when protein is required by the colony. Predation is costly, although costs are not as severe as in normal predator- prey interactions because aphids are clonal organisms. Instead, the loss of individual aphids is only a partial loss to the aphid colony, which effectively reproduces as one unit. Aphid colonies benefit through protection from predators, hygienic services, transport and shelter and the interaction with ants is often described as an overall mutualism (for reviews see:Way 1963, Delabie 2001, Stadler and Dixon 2005).

Ant-tended aphids are often well adapted for the mutualism. Large quantities of high quality honeydew are produced and retained on the abdomen for ants (Darwin

1   1859, Banks and Nixon 1958, Del-Claro and Oliveira 1993). Conversely, aphids that

2   are not ant-attended often retain defences such as evasion behaviour or deterrent traits

3   (Buckley 1987, Suzuki and Ide 2008, Tokunaga and Suzuki 2008). These different

4   adaptive strategies either increase or decrease encounter rates with ants and it appears

5   that tolerance and resistance type strategies respectively are being used. This is

6   explained in more detail below.

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8   In ant-tended aphids, honeydew quantity (Banks and Nixon 1958, Takeda, Kinomura

9   and Sakurai 1982, Del-Claro and Oliveira 1993), and quality (Yao, Shibao and

10   Akimoto 2000, Fischer and Shingleton 2001, Yao and Akimoto 2002), is actively

11   increased in the presence of ants. Production of low volumes, or low quality

12   honeydew leads to increased predation by ants, rather than tending (Edinger 1985,

13   Sakata 1995, Sakata 1999, Fischer, Hoffman and Wolfgang 2001). This conditional

14   predatory behaviour by ants could be viewed as a form of punishment, which

15   promotes stability in mutualisms (Pellmyr and Huth 1994, Kiers, Rousseau, West and

16   Denison 2003, Bshary and Grutter 2005, Edwards, Hassall, Sutherland and Yu 2006).

17   Punishment behaviour by ants alone, however, is only half the story. Aphids must

18   respond to such punishment, and they often appear to do so by modifying honeydew

19   quality to minimise costs of predation.

20   Predation by ants is an important cost of the interaction for aphids (Way 1963,

21   Offenberg 2001) and, thus, modifying honeydew serves as a means to decrease the

22   cost of the interaction for an aphid colony. Increased honeydew quality effectively

23   distracts ants from predating aphids, by increasing their relative value to ants as a

24   renewable honeydew source rather than as prey items. There are likely to be costs of

25   modifying honeydew (Fischer and Shingleton 2001, Yao and Akimoto 2001), just as

26   all defence traits have allocation costs (e.g. Strauss, Rudgers, Lau and Irwin 2002). If

27   the benefits of distracting ant predation more than offset these costs, however, than

28   the strategy is feasible. Indeed a number of aphid species appear able to modify

29   honeydew composition (Fischer and Shingleton 2001). Considering the effect this

30   modification of honeydew has on the encounter rate between the aphid colony and the

31   ants, there will clearly not be a *reduction* in encounter rate. Indeed, the recruitment of

32   ant foragers is positively correlated with the value of a food source (Bonser, Wright,

33   Bament and Chukwu 1998, Katayama and Suzuki 2003, Mailleux, Deneuborg and

34   Detrain 2003, Portha, Deneuborg and Detrain 2004), and high quality honeydew-

producing aphids attract more ants per aphid (Fischer, Hoffman and Wolfgang 2001, Fischer, Volkl and Hoffman 2005). Thus, phenotypic plasticity of honeydew production in aphids is a trait that reduces the overall cost of interacting with ants i.e. a 'defence' trait. Furthermore, the reduced interaction cost is achieved without a reduction in overall encounter rate. Therefore we can describe it as a tolerance rather than a resistance trait.

In contrast to the tolerance defence strategies described above, non ant-tended aphids may resist encounters with ants by using resistance traits. Such traits are well documented and include *evasion* behaviour, e.g. dropping from the plant triggered by alarm pheromones (Roitberg and Myers 1978, Arakaki 1989, Losey and Denno 1998, Suzuki and Ide 2008) or increased alate production (Kunert, Otto, Röse, Gershenzon and Weisser 2005, Mondor, Rosenheim and Addicott 2005). Alternatively, aphids may employ *deterrence* traits, e.g. waxy coverings, hard sclerotized cuticles, cornicle secretions, aphid toxicity or kicking behaviour (Buckley 1987, Bristow 1991, Dixon 1998).

Overall, if ant attendance is not beneficial for aphid species, it is likely that they will evolve traits to minimise ant attendance. Such traits are resistance traits. In contrast, aphids which do benefit in some part may be selected for tolerance traits. After this initial selection for a particular defence strategy, evolutionary trajectories will split, with divergence reinforced through positive feedback processes; resistance traits intensify coevolutionary arms races, while tolerance traits facilitate stable mutualistic coevolution. Ecological factors may determine the initial direction of splitting (see Stadler and Dixon 2005, for explanations of ant-attendance), yet once an evolutionary pathway is commenced upon, the type of defence strategy, resistance of tolerance, will be important in reinforcing the trajectory through positive feedback processes. As such, tolerance traits such as plasticity in honeydew production may facilitate the mutualism between ants and aphids. In the absence of tolerance traits, aphids would be unable to reduce the costs inherent in the interaction without using resistance. Such resistance would reduce selection for continued mutualistic co-adaptation, thereby reducing the stability of the interaction.

Conclusion

To summarise, we have proposed the idea that defence traits may be important in maintaining stability in mutualistic interactions. Tolerance traits allow the costs inherent in an interaction to be minimised, whilst still allowing the overall interaction to be maintained. In contrast, resistance traits act to reduce synchrony in space and time with a partner lineage. Thus, the type of defence strategy used by a species may affect the likelihood of transition of an interaction into mutualism, as well as promoting stability within mutualisms. Phenotypic plasticity of honeydew production by aphids could be an example of how tolerance traits can facilitate mutualistic interactions. Many factors, such as aphid physiology and ant nutritional requirements, determine the initial coevolutionary trajectory of an interaction, but positive feedback in defence traits can lead to further divergence.

Whilst resistance traits promote escalating arms races, tolerance traits may pave the way for mutualistic coevolution. Indeed, the adoption of tolerance traits may be one of the primary mechanisms in the formation of persistent cooperative interactions between species. Differences in tolerance between species have been shown to influence community structure (Stowe, Marquis, Hochwender and Simms 2000) and this may be even more so if tolerance traits lead to mutualisms which fundamentally shape communities (Christian 2001, Stachowicz 2001, Gomulkiewicz, Nuismer and Thompson 2003, Hay, Parker, Burkepile, Caudill, Wilson, Hallinan and Chequer 2004). We should highlight that this theory is very provisional and would benefit from further theoretical work investigating the evolution of tolerance; for example, by considering which factors promote tolerance over resistance strategies. Immediate candidates are the direct allocation costs of traits and also the cost of interacting with antagonists, with costly interactions selecting for resistance based strategies. To summarise, the study of tolerance has previously been restricted to antagonistic interactions. We suggest that broadening our consideration of tolerance defences to encompass mutualistic interactions will allow a better understanding of species interactions.

Acknowledgements

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