

Understanding mutualism when there is adaptation to the partner

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Summary

1 A mutualism is a mutually beneficial interaction between individuals of two species. Here we show that the degree of benefit resulting from an interaction depends on whether adaptation within the mutualism is considered.

2 A species' *proximate response* measures the short-term effect of addition or removal of the partner species, without allowing for any adaptation. We define a *proximate mutualism* as an interaction in which removal of each partner results in a decreased performance of the other, i.e. both species show a positive proximate response to the presence of the partner.

3 A proximate mutualism might, however, only reflect evolved dependence (i.e. the species has lost its ability to perform well without the partner). Some authors therefore insist on an ultimate criterion, regardless of the use of proximate responses in almost all empirical studies.

4 A species' *ultimate response* measures the long-term effect of adding or removing the partner species, thus allowing the focal species to adapt. In an *ultimate mutualism* neither partner could ever have performed as well without the other. In other words, a mutualism is called ultimate if both species show a positive ultimate response to the presence of the partner. Despite the conceptual attractiveness of this definition, ultimate responses are difficult to measure, rendering its use operationally problematic.

5 *Mutualistic evolution*, the evolution of a trait that is costly to the bearer but beneficial to its partner, is not, paradoxically, a necessary consequence of either proximate or ultimate mutualism. Another counterintuitive result is that even obligate mutualisms are not necessarily ultimate interactions.

6 We conclude that the proximate response is the only workable criterion for mutualism. Our understanding of mutualism, however, requires further evaluation of how evolved dependence may be responsible for such responses.

7 These concepts clarify the ongoing debate about whether plant–herbivore interactions can be considered as mutualistic.

8 This is not a semantic case of hair splitting: naïve aspects in current views of mutualism need revision. In most, if not all, interactions now considered as mutualisms, some of the measured benefits are likely to result from evolved dependence, rather than what we would like to consider as ultimate benefits.

Key-words: adaptation, coevolution, evolved dependence, mutualism, overcompensation, plant–herbivore interaction, proximate response, ultimate response

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Introduction

Mutualisms are widespread in nature (Boucher *et al.* 1982; Bronstein 1994b; Menge 2000; Richardson *et al.* 2000; Stachowicz 2001). However, although about a quarter of ecological studies are devoted to mutualism (Bronstein 1994b), our understanding of and theoretical insights into this type of interaction are limited (Bronstein 1994b). One factor that might contribute critically to this gap is that in a mutualistic interaction, there is usually adaptation to the partner species, and this may lead to ambiguity. Here we ask how one can determine whether or not a particular interaction in a given environment is mutualistic, bearing in mind that the same interaction might be classified differently in a different environment (Bronstein 1994a). Such environmental dependence is called conditional mutualism (all key terms are defined in Appendix 1).

We set the scene by describing a parasitic relationship that evolved into an obligate mutualism (Jeon 1972). When *Amoeba discoides* was first infected with bacteria, it showed heavy mortality, small size, slow growth, slow clone formation and high sensitivity to adverse conditions. However, the amoeba and the bacteria coevolved until, 5 years after the initial infection, the adverse effects of the bacteria had disappeared and neither organism could now survive without the other! The interaction is thus a clear example of a mutualism (proximate mutualism as defined in Appendix 1) in that both partners clearly derive a benefit from the partner's presence: the ability to survive. However, is it possible that the amoeba would have been better off had the bacteria never been there? In other words, does the bacterium provide any 'real' benefit to the amoeba and should the interaction be viewed as a mutualism at all (ultimate mutualism as defined in Appendix 1)?

We consider three different criteria that can be used to test for mutualism, i.e. the proximate response (in essence, the short-term effect of removal of the partner on performance, but see Appendix 1 for a full definition), the ultimate response (the long-term effect of removal of the partner on performance, allowing for adaptation to the presence and absence of the partner) or mutualistic evolution (evolution of a trait that is costly to the bearer but beneficial to its partner). Unfortunately, there is likely to be a conflict between what is actually assessed in most tests for mutualism, i.e. what we call a proximate response, and what many of us would like mutualism to mean, i.e. an ultimate mutualism. Although each of the criteria has been used previously by different authors, they have never been clearly defined and contrasted. Doing so provides the platform for a thought-provoking discussion about what mutualism means and the demonstration of several counterintuitive results.

We discuss the specific application of our ideas to the debate about plant–herbivore interactions and their broader implications for other systems. Some plants have been shown to overcompensate, in the sense that their fitness is increased by herbivore damage: the

controversy that has ensued in the literature is whether this implies that such plants actually benefit from herbivory and that the plant–herbivore interaction must therefore be considered mutualistic.

Proximate mutualism

One classical experimental approach to testing for mutualism is to evaluate the performance of a species before and after its partner has been removed, or has been kept at low density (Schoener 1983; Bender *et al.* 1984; Krebs 1985). This comparison defines what we call the *proximate response* of a species to the removal of its partner, and measurement of such a response is the criterion for identifying a *proximate mutualism* (Fig. 1 and Appendix 1). It is important to stress that, in this definition, the performance of the *same* genotype (or group of genotypes) is compared with and without the partner species. The proximate response might depend on the genotype considered, and, notably, on the status of its adaptation to the partner (Fig. 1).

Bronstein (1994b) described the rationale underlying such experiments as follows: 'mutualists were excluded or added ... For example, many pollination studies examined plant success after all but a single visitor species were excluded (Herrera 1987) ... Nearly all experimental studies of plant–ant protector mutualisms involved excluding the ants in order to measure their benefit to the plant (Smiley 1986; Koptur & Lawton 1988)'. Mutualistic or parasitic effects of mycorrhizal associations or of leaf endophytes have also been assessed by comparing the proximate responses of the plants, i.e. the performance of a plant genotype or population with and without the partner (Faeth & Sullivan 2003; Klironomos 2003).

Evolved dependence

The decreased performance observed when a partner is removed might, however, simply be due to the focal species being adapted to the presence of its partner, having thus compromised its ability to perform well in the partner's absence. In the context of endosymbioses, such an effect has been called *evolved dependence* (Douglas & Smith 1989).

It is important to emphasize that evolved dependence is likely to happen in any type of association where there is adaptation, i.e. it can occur independently of whether or not an association is obligate. Evolved dependence is, in principle, quantifiable as the performance difference between the genotype that is adapted to the partner's absence and the genotype that is adapted to its presence, both measured in the absence of the partner (Fig. 1, Appendix 1). This reflects both the cost of traits that have evolved as an adaptation to the partner's presence and the disadvantage of losing any traits that were adaptive in the absence of the partner (the latter only being apparent as a cost when the partner is removed). Operationally, the length of time that partners

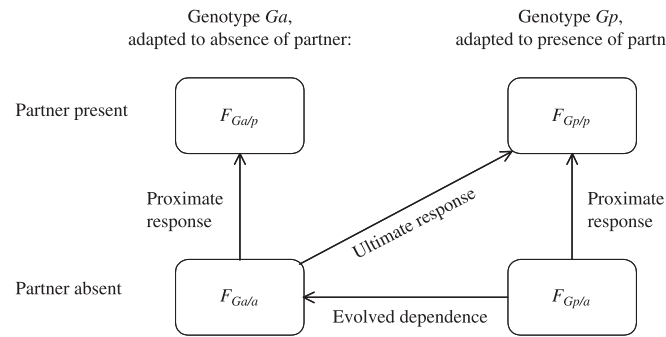


Fig. 1 Performance of a genotype adapted to the absence of its partner (left column), a genotype adapted to the presence of its partner (right column), both in the presence of the partner (upper row), and in the absence of its partner (lower row). Differences between these four performances measure the responses discussed in the text. The proximate response of the organism to partner removal is measured for individual genotypes, as $F_{Galp} - F_{Gala}$ for the genotype adapted to the partner, and as $F_{Gplp} - F_{Gpla}$ for the genotype adapted to the absence of the partner. The ultimate response of the organism to partner removal is measured as $F_{Gplp} - F_{Gala}$, i.e. as the difference between the performance in the presence of the partner of a genotype that evolved with the partner and the performance in the absence of the partner of a genotype that evolved without the partner. Evolved dependence is measured as the difference between the performance without the partner of a genotype that evolved without the partner and the performance without the partner of a genotype that evolved with the partner, $F_{Gala} - F_{Gpla}$. Note that the ultimate response of a genotype adapted to the partner equals its proximate response minus the evolved dependence.

have been in ecological contact with each other (or the length of time they have been separated) can be used as a rough indicator of the expected degree of mutual adaptation.

Thus the proximate response of a genotype is bound to depend on the status of its adaptation to the partner. A low performance when the partner is removed can occur simply because the genotype is not adapted to this situation, i.e. it shows evolved dependence rather than the 'real benefit' implied by a naive view of mutualistic interactions.

Ultimate mutualism

To understand whether evolved dependence is responsible for an observed proximate mutualism between two species, or whether there is actually an ultimate benefit from the interaction, we have to ask whether the focal species performs better than it would ever have done without the other species. We thus have to consider the *ultimate response* of a species to its partner, measured by comparing the performance of two *different* genotypes (or groups thereof): the performance, in the partner's presence, of a genotype adapted to the partner, is compared with the performance, in the partner's absence, of another genotype adapted to this absence. Although there are practical difficulties in measuring such responses, an *ultimate mutualism* can be defined as an interaction in which each partner shows a positive ultimate response to the presence of the other (Fig. 1, Appendix 1).

The proximate response of a population adapted to its partner is the sum of its ultimate response and its evolved dependence. Therefore, if a population derives an ultimate benefit from a partner species, it is also likely to derive a proximate benefit from the interaction. However, the reverse is not true as evolved dependence could be the sole cause of a proximate benefit, in which

case the population will derive no ultimate benefit whatsoever from the association.

Evolved dependence is likely to be important for partners with a long history of coevolution, and some of these interactions are therefore likely to involve proximate mutualisms that are not ultimate mutualisms.

Relatively few authors adopt the ultimate response as their criterion for assessing the benefit of an interaction. Examples from the plant-herbivore literature will be described later but it was also used by Roughgarden (1975) in a model for the evolution of a symbiosis between fish and anemones. Assuming the ancestral state of fish to be free living, Roughgarden assessed the benefit of the symbiosis as the difference between the fitness of the free-living genotype and the fitness of the symbiotic genotype with an anemone. The model nevertheless assumed a strong evolved dependence in that the reproductive output of the symbiotic genotype is much reduced when it cannot find a host anemone, or when its host anemone dies.

MEASUREMENT OF ULTIMATE RESPONSES

Measuring ultimate responses requires tests both on a genotype that is adapted to the presence of the partner and on a genotype that is adapted to its absence. As there is no point in defining quantities that are not measurable in practice, the status of adaptation to the partner must be assessed pragmatically. It may be impossible to assess whether adaptation has reached an evolutionary endpoint and, in some cases, this might not even exist (Dieckmann *et al.* 1995; Gomulkiewicz *et al.* 2000; Thompson & Cunningham 2002). This should not, however, prevent evaluation of an ultimate response based on the current status of adaptation, as this can be roughly approximated from the length of co-evolutionary history. The strength of selection imposed by a species on its partner would be a better proxy for the status of adaptation, but it cannot easily be quantified.

Three cases can be distinguished:

- We may have access to an ancestral state that is not adapted to the partner. Alternatively, if the organism is fast evolving and is viable without the partner, it is feasible to select for adaptation to the partner's absence. Performance measurements can then be made under the appropriate conditions. Unfortunately, populations experimentally adapted to the partner's presence or absence might inadvertently have been subjected to additional, unrelated selective pressures.
- Even though there may be no access to a suitable ancestral state, separate populations of the focal organisms may exist with histories of evolution with and without the partner and these can be compared, provided sufficient replicates exist. Again other factors are likely to covary with the partner's presence or absence.
- There may be no access to an ancestral state, the organism may not be viable without the partner or, even if it is viable, its generation time may be too long for experimental adaptation to the partner's absence to be feasible. Ultimate responses cannot then be measured. However, if there is sufficient genetic variation in the species, it may still be possible to search for genetic trade-offs between the focal species' performance with and without the partner, and thus to establish indirect evidence for evolved dependence.

Douglas & Smith (1989) discuss in detail the difficulties of measuring ultimate responses in endosymbioses.

Although the concept of ultimate mutualism is very satisfactory conceptually, it may well prove unrealistic in terms of measurements. Those authors who accept only this definition of mutualism, and discard any alternative based on proximate responses, apparently overlook the difficulties of measuring ultimate responses, as well as the fact that most empirical work has only measured proximate responses.

An obligate mutualism is not necessarily an ultimate mutualism

It is somewhat counterintuitive that an obligate mutualism is not necessarily an ultimate mutualism. Long-term infection of *Amoeba discoides* with a parasitic bacterium led to the adverse effects of the bacteria disappearing (Jeon 1972; see Introduction). Both organisms became dependent on the other for survival, resulting in a mutualism that is both proximate and obligate. Importantly, however, the proximate benefit derived by the amoeba from the interaction is probably due to evolved dependence. This may have led to the amoeba losing traits that made it adapted to the absence of the bacteria and there is no evidence for the interaction providing an ultimate benefit to the amoeba; the ability to tolerate infection is essentially a neutral effect.

Another example involves *Wolbachia*, intracellular bacteria that infect a number of invertebrates. In arthropods, these bacteria are rarely found to be beneficial to their hosts and thus provide a striking example of selfish cytoplasmic elements. Despite physiological

costs, or even virulence, they are able to maintain themselves through induced modifications to host reproductive biology. In the obligate mutualism with the parasitoid wasp *Asobara tabida* Nees (Hymenoptera, Braconidae), female wasps cannot reproduce after removal of *Wolbachia* because they do not produce mature oocytes (Dedine *et al.* 2001). The wasp, or its ancestor, may have become associated with a *Wolbachia* that produced a factor necessary for wasp oogenesis. In the partnership, the wasp does not need to produce this costly factor itself, but loss of this capacity resulted in its becoming totally dependent on the bacteria for reproduction. Similar losses of function have been reported in other insect–*Wolbachia* interactions. There are several examples in which induction of parthenogenesis resulting from *Wolbachia* infection can be reversed by curing the infection (Stouthamer 1997), but in some cases the host species can no longer function successfully as a sexual taxon due to adverse changes in male and/or female traits (Hunter 1999; Arakaki *et al.* 2001; Gottlieb & Zchori-Fein 2001). Gottlieb & Zchori-Fein (2001) argue that, because sexual reproduction has ceased, selection on sexual traits has been removed, leading to disappearance of or reduction in these traits. They suggest that manipulation of the reproductive system to induce parthenogenesis, allows the bacteria to capture a host for its own transmission benefit, while leaving the host with no other means of reproduction. These cases are clear examples of obligate proximate mutualisms, where the main benefits for the host come from evolved dependence. We suggest that these interactions are unlikely to be ultimate mutualisms, although this has not yet been tested.

Even interactions that pass through a phase of ultimate mutualism may well have ultimate costs that escalate over evolutionary time. Species that evolve an extreme dependence on their partner, and are therefore committed to the interaction whatever its costs (Pellmyr *et al.* 1997), are particularly likely to be stuck in the interaction even if it ceased to be an ultimate mutualism. Johnson *et al.* (1997) argue that plants that are highly dependent on mycorrhizas for nutrient uptake might have a greater risk of mycorrhizal parasitism in highly fertilized systems because they might not closely control 'unnecessary' root growth or rate of colonization. It is possible that such plants might be 'trapped' in this obligate interaction even when conditions change and the interaction no longer brings any ultimate benefit.

Comparing proximate and ultimate responses

Almost all costs and benefits measured in empirical studies have been proximate (i.e. the same group of genotypes was compared with and without the partner; Bronstein 1994b). New and interesting research directions could thus be opened up by investigating ultimate costs and benefits (where possible) and by looking for trade-offs between genotypes differentially adapted to the partner's absence and presence.

A very important question in mutualism research is the evolution and maintenance of mutualisms in the presence of 'cheaters' (Bronstein 2001; Law *et al.* 2001; Yu 2001; Ferriere *et al.* 2002; Johnstone & Bshary 2002; Denison *et al.* 2003; Freckleton & Cote 2003; Hoeksema & Kummel 2003). Measuring the costs induced by the presence of cheaters and contrasting proximate and ultimate costs might be a key element to further understanding this question. For instance, nectar robbers damage floral parts and take resources without effecting pollination (Inouye 1980). Most removal experiments assess the cost of robbers on the female fitness of the plant by experimentally removing robbers, thus assessing the proximate cost of their presence. The ultimate cost, however, is likely to be even higher. Roubik *et al.* (1985) showed that the flowers of a tropical forest understorey treelet, *Quassia amara*, had lower corolla length and nectar production on an island where no nectar robbers were found, suggesting that their absence leads to selection against these traits. The performance of plants adapted to robbers is therefore suboptimal and evolved dependence will increase the ultimate cost of robbers' presence above the corresponding proximate cost. The performances of different genotypes in the presence and absence of robbers needs to be compared to establish whether they show variation in their adaptation to the presence of cheaters.

Evolution in a mutualism

The concept of *mutualistic evolution* (our third criterion for assigning a mutualism, see Appendix 1) is key to many discussions about mutualism. Evolution of investment in a partner has a direct cost to the bearer but, other things being equal, increases the performance of both parties. It is important to realize that not all adaptations to a mutualistic partner qualify as mutualistic evolution, because traits may also evolve to either allow or prevent better exploitation of the partner. Certain functions may also be lost evolutionarily if they are provided more efficiently by the partner (Connor 1995).

WHERE DOES THE BENEFIT OF AN INTERACTION COME FROM?

When defining proximate and ultimate mutualism, we used criteria based on the net effect of the presence of the partner, rather than descriptions of the physiological and ecological processes through which benefits are gained (i.e. effect- rather than process-based definitions; Abrams 1987). When considering mutualistic evolution it is interesting to distinguish between different categories of benefit gained from an interaction. Connor (1995) contrasts *by-product benefits*, occurring incidentally at no cost to the donor (as for two plants accidentally growing together with one taking advantage of the other's protective thorns), with *purloined benefits*, obtained by exploiting the partner (as a predator would), and *invested benefits*, obtained despite a direct cost because the partner is giving something for a return.

Proximate and ultimate mutualisms can result from benefits of any of these types. Several authors, however, have demanded evidence of the evolution of invested benefits in order to demonstrate that an interaction is 'truly' mutualistic (Belsky *et al.* 1993; Agrawal 2000). We use simple cases of two interacting species coevolving in a constant environment to argue that such evolution does not necessarily happen in either proximate or ultimate mutualisms, and that it can occur even towards an exploitative partner. Co-evolution is often diffuse (Inouye & Stinchcombe 2001; Agrawal & Van Zandt 2003) and theories taking into account this complexity therefore need to be developed (Stanton 2003; Loreau *et al.* 2004), but this is beyond the scope of the present paper.

ANTAGONISTIC STRATEGIES CAN BE SELECTED FOR IN MUTUALISTIC INTERACTIONS

A mutualistic strategy might be counter-selected in a proximate or ultimate mutualism. It is well known that evolution of investment in the partner requires that 'the partner must reciprocate and that the reciprocated benefit must be captured by the initial giver or its offspring' (Yu 2001). A trait leading to investment in the partner will not therefore evolve if its beneficial effect has to be shared with a large number of conspecifics. Thus the evolution of fruit abortion in the senita cactus or in yuccas as a means of decreasing seed predation by their pollinators only occurs if the pollinator population is localized on the individual plant (Holland & DeAngelis 2002). If the benefit of an investment in the partner is uniformly distributed over all conspecifics, there might even be selection for an antagonistic strategy, as we show below for a plant–herbivore interaction.

SELECTION CAN FAVOUR INVESTMENT INTO AN EXPLOITING PARTNER

A possible scenario involves evolution of a trait that benefits the bearer by protecting it against predation. The majority of the estimated 6000 species of Lycaenid butterflies have associations with ants that range from mutualism to parasitism (Pierce *et al.* 2002). A standard interpretation of the mutualistic association is that lycaenid larvae produce secretions in order to attract ants and benefit from the protection the ants provide against parasitoids. Malicky (1970), however, suggested that the secretions might, instead, prevent predation by ants, in which case they would be an example of an investment in an exploiting partner.

Plant–herbivore interactions

PROXIMATE RESPONSES TO HERBIVORE REMOVAL

Experimental studies have demonstrated that, under some conditions, herbivory leads to increased plant fitness.

Lifetime reproductive output (seed production of monocarpic plant species, controlling for seed weight and germination potential) was increased by grazing or cutting for some populations of *Ipomopsis aggregata* (Paige & Whitham 1987; Paige 1992; Gronemeyer *et al.* 1997) and *Gentianella campestris* (Lennartsson *et al.* 1997, 1998; Huhta *et al.* 2000b; Juenger *et al.* 2000). Other monocarpic species can show increased seed production following moderate cutting under field conditions (Huhta *et al.* 2003) or artificial conditions such as reduced competitive pressure and/or fertilizer application (Benner 1988; Alward & Joern 1993; Huhta *et al.* 2000a). Some authors (Vail 1994; Agrawal 2000) accept this evidence as confirmation of a possible benefit of the plant from herbivory, leading to the claim that this interaction may be a mutualism (proximate mutualism).

EVOLVED DEPENDENCE OF PLANTS TOWARDS THEIR HERBIVORES

Increased seed production in overcompensating plants often results from the release of apical dominance and from the production of numerous tillers (Paige & Whitham 1987; Benner 1988; Lennartsson *et al.* 1997, 1998; Paige 1999; Strauss & Agrawal 1999; Huhta *et al.* 2000b; Juenger *et al.* 2000). If the probability of herbivory is high, a plant that produces multiple shoots from the beginning of the season will lose them all to the herbivore (Crawley 1987). If, however, herbivory only occurs during a short period, then damage by herbivores could serve as a signal that the risk of herbivory soon will be over: activation of dormant meristems following herbivory will then have a selective advantage (Vail 1992; Tuomi *et al.* 1994b). Several models suggest that plants adapted to herbivory should have developed mechanisms for resource mobilization that are triggered by herbivory (Vail 1992, 1994; Mathews 1994; Tuomi *et al.* 1994b; Nilsson *et al.* 1996a, 1996b; Jaremo *et al.* 1999; Simons & Johnston 1999; Lehtila 2000). Such adaptation leads to low reproduction in the absence of herbivory, *simply because the plant genotype concerned is not adapted to a situation without herbivores*, and there is a trade-off between the ability of a plant to perform with and without herbivores. In the presence of herbivores, it is advantageous to wait before allocating resources to growth, but in their absence the trait is disadvantageous and plants should instead allocate all their resources to growth as soon as possible.

Evolved dependence may well explain the proximate benefit in many plant–herbivore interactions. In *Gentianella campestris*, the plant's ability to produce more seeds after herbivore damage only occurs in populations adapted to either herbivory or mowing (Lennartsson *et al.* 1997, 1998). Similarly, the ability to tolerate herbivory was negatively correlated with fitness in the absence of herbivory in *Ipomoea purpurea* (Tiffin & Rauscher 1999).

Because overcompensation is likely to result from evolved dependence rather than any other mechanism

of ultimate benefit, some authors do not accept the proximate response of overcompensation as sufficient proof that plants might benefit from herbivory (Belsky *et al.* 1993; Mathews 1994; Tuomi *et al.* 1994b; Jaremo *et al.* 1999).

ULTIMATE MUTUALISM IN PLANT– HERBIVORE INTERACTIONS

There are theoretical arguments that plants may incur ultimate costs from plant–herbivore interactions. Vail (1992) built a model showing that plants benefit from herbivory because plants adapted to herbivores perform better when they are present. However, he noted that although removal of herbivores reduces fitness in the short term, ‘that would simultaneously impart a selective pressure ... and thus raise fitness in the long run’. Mathews (1994) criticized Vail's interpretation: ‘although Vail speculates about the benefits of herbivory, his model in fact contradicts him because plant fitness is higher in the absence of herbivory than anywhere else’. For Mathews, the proximate criterion is not valid for testing benefits from herbivory: there needs to be an ultimate benefit resulting from the presence of herbivores. Other recent studies seem to show some convergence towards using the ultimate response criterion (Tuomi *et al.* 1994a, 1994b; Nilsson *et al.* 1996a, 1996b; Jaremo *et al.* 1999; Simons & Johnston 1999; Stowe *et al.* 2000), and rejecting the validity of a proximal response criterion.

Nor is there empirical evidence for plant–herbivore interactions leading to an ultimate benefit for the plants. Jaremo *et al.* (1999) measured the ultimate response of *Gentianella campestris* to herbivore removal, using existing data to compare populations that have evolved with the herbivore with populations that have evolved without it, and detected neither an ultimate benefit nor an ultimate cost. In a different study, the comparison of reaction norms of maternal lines from different populations also failed to show any trade-off between fitness in the absence of herbivory and the ability to compensate for herbivory (Juenger *et al.* 2000), suggesting that the response of this plant to herbivores is ultimately neutral.

MUTUALISTIC EVOLUTION

Belsky *et al.* (1993) define a ‘mutualistic plant’ as a plant that ‘makes some portion of their bodies available to herbivores’ (i.e. a plant that invests in the herbivore), whereas an ‘antagonistic plant’ defends itself against herbivores. They argue that if plant–herbivore interaction were mutualistic, then we should witness the evolution of mutualistic plants, implying mutualistic evolution through which the plant evolves to invest in its herbivore. However, we argue that this is not necessarily the case.

If herbivores promote the efficient recycling of nutrients and if this has a positive effect on plant fitness (de Mazancourt *et al.* 2001), then plants receive a benefit

from the presence of herbivores. The more efficient the herbivore is at recycling nutrients, the more benefit there is to the plant, and at high herbivore recycling efficiencies the interaction could well be a proximate or even an ultimate mutualism. However, the benefits of nutrient cycling tend to be distributed amongst all plants and as mutualistic plants do not therefore receive a one-on-one benefit they experience a direct cost from herbivory. It can be shown that the more efficient the herbivore becomes at recycling, the greater is the extent to which defended plants benefit more than undefended plants from these nutrients. Therefore, the more herbivores recycle, the more selection there is for antagonistic plant strategies and plant defences thus increase. At the same time, nevertheless, the interaction can become a proximate and even an ultimate mutualism as long as herbivores conserve nutrients in the system to an extent that enables plants to perform better on the whole.

Although there have been many empirical studies on the effects of herbivores on nutrient cycling (Floate 1981; Carpenter & Kitchell 1984; Detling 1988; Ruess & McNaughton 1988; Jarvis *et al.* 1989; Ruess *et al.* 1989; Seagle *et al.* 1992; Chaneton *et al.* 1996; Wilson & Jefferies 1996; Pastor & Cohen 1997; Ritchie *et al.* 1998), none has yet studied the net effect of herbivory on plant fitness and the resultant selection pressure on plants. We cannot therefore assess if mutualistic interactions with antagonistic evolution between plants and herbivores occur in nature.

Conclusions

So, how can we identify a mutualism when there is adaptation to the partner? If we have to choose only one of the three contrasting definitions, it has to be that of proximate mutualism, as discarding this criterion would abandon the core evidence for most studied examples of mutualism. However, in choosing this criterion, we must acknowledge the potential importance of evolved dependence between partners as a valid mechanism for creating a benefit. In the plant-herbivore debate, this means that we have to accept evidence of overcompensation as evidence that plants indeed benefit from herbivory (provided that overcompensation occurs as a result of realistic levels and patterns of herbivory), however irritating and counterintuitive this might be. More empirical and theoretical studies should take into account evolved dependence as a possibly crucial mechanism generating mutualism.

What many people would intuitively like to call mutualism is similar to ultimate mutualism, or 'true' mutualism (as stated by Agrawal 2000), i.e. a mutualism that does not stem solely from evolved dependence. Unfortunately, however, an ultimate response cannot even be meaningfully described in many classical examples of mutualisms. Because of major difficulties involved in its measurement, we believe that the ultimate response will tend to remain an abstract, albeit

occasionally useful, concept. Moreover, even obligate mutualisms are not guaranteed to be 'true' or ultimate mutualisms.

It appears possible to resolve the plant-herbivore controversy by adopting a criterion of ultimate rather than proximate benefit (Järemo *et al.* 1999), thus rejecting the proximate criterion of overcompensation. We contend that this is not satisfactory, given the importance of the proximate criterion in most classical examples of mutualism and argue that we should instead recognize the potentially important role of evolved dependence in all mutualisms.

Finally, the analysis of adaptations that can bring about, maintain or jeopardize mutualistic interactions needs to be disentangled from the criteria for mutualism itself. Traits that favour or harm a partner might evolve in any type of interaction and defining mutualism through mutualistic evolution therefore seems of limited utility.

Differentiating between our three criteria allows us to focus on new and stimulating research questions. For many interactions that are currently considered mutualistic it will be illuminating to evaluate empirically (a) whether there is adaptation to the presence of the partner, (b) which mechanisms are responsible for evolved dependence and its selection, (c) how evolved dependence contributes to proximate benefits, and (d) how proximate and ultimate benefits affect the mutualistic or antagonistic evolution of traits.

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Appendix 1: Definition of key terms

Performance: to compare the performance of organisms under different conditions (with or without partners), we need an absolute measure of performance, rather than a relative one. What measure to use is not a trivial question and there are several possibilities.

(1) *Absolute fitness* of an individual, i.e. its lifetime reproductive success (LRS). This always equals 1 when populations are at steady state, so that care must be taken in setting the conditions under which lifetime reproductive success is measured (as described below). Proxies of absolute fitness can sometimes be used.

(2) *Short-term population growth rate.* This is a good proxy of lifetime reproductive success under conditions of repeated disturbance, during which a population tends to remain in an exponential growth phase.

(3) *Long-term population size.* This may be a proxy for absolute fitness for populations close to steady state.

Discrepancies between the different measures are discussed in Abrams (1987) and van Baalen & Jansen (2001).

Proximate response: difference in performance of a genotype (or group thereof) before and after short-term removal (or addition) of the partner species. Note that the performance of the same genotype (or group thereof) is therefore compared under two conditions, one of which it might not be adapted to.

Measurement. If performance is measured as lifetime reproductive success, the focal species' density after removal must be kept at its value before removal. We can then consider the focal population with its partner, with $LRS = 1$, before removing the partner, and measuring the new lifetime reproductive success, LRSP. The proximate response to removal is $LRSP - 1$.

Proximate mutualism: interspecific interaction in which removal of each partner results in a decreased performance of the other. It is characterized by negative proximate responses of each species to the removal of the other species. Such negative proximate responses can be due to 'real' (i.e. ultimate) benefits but, alternatively, may merely reflect evolved dependence resulting from adaptation to partner.

Evolved dependence: through adaptation to the presence of an interacting partner species, a population might lose its ability to perform well in the absence of its partner. Evolved dependence measures the loss of performance

of a focal population in the absence of a partner due to its adaptation to the presence of the partner.

Measurement. LRSP (lifetime reproductive success of the focal population in the absence of the partner) can be measured as for a proximate response (see above). We can then replace every individual in the focal population with a genotype adapted to the absence of the partner, and measure the new LRSU. The evolved dependence is $LRSU - LRSP$.

Ultimate response: difference in performance before and after 'long-term' removal (or addition) of a partner species, allowing for adaptation to take place. Performance of a genotype (or group thereof) adapted to the presence of the partner is measured in the presence of the partner, and compared with the performance of a genotype (or group thereof) adapted to the absence of the partner measured in the absence of the partner.

Measurement. The focal species' density in the presence and absence of its partner must be kept the same. The focal population with its partner has $LRS = 1$. LRSU (the lifetime reproductive success of an unadapted genotype) is measured as described for evolved dependence and the ultimate response to removal equals $LRSU - 1$.

Ultimate mutualism: interspecific interaction in which each partner could never have performed as well without the other, even if it was adapted to the absence of the partner. In other words, ultimate mutualism is characterized by negative ultimate responses of each species to the removal of the other species.

Mutualistic evolution: evolution of a trait that is costly to the bearer but beneficial to its partner in a proximate mutualism (investment in a partner *sensu* Connor 1995). Note that adaptation to the partner does not necessarily imply mutualistic evolution; for example, there can be evolution of traits that allow better exploitation of the partner.

Obligate mutualism: interaction in which the removal of the partner results in death or complete loss of reproduction in the focal species. The focal species therefore derives a proximate benefit from the interaction, as its proximate response to partner removal is maximally negative. In many cases, ultimate response to partner removal cannot be measured. The alternative is *facultative mutualism*, where partner removal reduces performance, but does not annihilate it.

Conditional mutualism: an interaction that can be mutualistic (proximate or ultimate) under specific environmental conditions (Bronstein 1994a).