

## SPECIAL FEATURE – ESSAY REVIEW FACILITATION IN PLANT COMMUNITIES

# The evolution of facilitation and mutualism

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### Summary

1. While the relationship between facilitation and competition has been explored extensively in recent years, there is also a natural link between facilitation and mutualism, as both are interspecific interactions that confer benefits. Yet, the relationship between these two interactions has been minimally explored.

2. Here, I explore parallels and differences between mutualism and facilitation. Five focal areas organize current research on mutualism evolution: trait evolution; the continuum from specialization to generalization; the evolutionary origins and maintenance of the interaction; co-evolution of partners; and the prevalence and implications of cheating. These foci are also helpful for investigating how facilitation evolves, a much less explored issue.

3. Testable hypotheses regarding the evolution of facilitation include the following: selection should be stronger on traits of facilitated species than on traits of facilitators; facilitative interactions with mutualistic (+ +) and commensal (+ 0) outcomes should exhibit greater evolutionary stability than those with antagonistic (+ –) outcomes; co-evolution should be possible in mutualistic and antagonistic facilitation only; when co-evolution occurs, it should produce a geographic mosaic of interaction outcomes; and antagonistic facilitation could lead to selection on facilitators to either escape or to tolerate the neighbours that benefit from them.

4. *Synthesis.* Three gaps in our knowledge currently impede progress on evolutionary questions surrounding facilitation. First, reciprocal effects are rarely investigated; facilitation might evolve like mutualism, commensalism or antagonism, depending on effects on the facilitator species. Secondly, the genetics of relevant traits are not yet well explored; the traits themselves are better known for facilitator species than for the facilitated, which are more likely to evolve in the context of the interaction. Finally, the fitness costs and benefits associated with facilitation have rarely been measured. Filling these gaps should permit rapid progress in understanding how facilitation arises, persists and evolves.

**Key-words:** co-evolution, community, evolution, facilitation, mutualism, plant–plant interactions, positive interactions, specialization

### Introduction

Positive interactions are ubiquitous in natural communities, although it is now widely recognized that they have been relatively ignored by ecologists and evolutionary biologists (Bronstein 2001a; Bruno, Stachowicz & Bertness 2003; Callaway 2007; Brooker *et al.* 2008). This statement holds equally true for two rather different kinds of beneficial interactions, mutualism and facilitation. Mutualisms are reciprocally positive interactions between pairs of species. Facilitation has been defined as an interaction in which the presence of one species alters the environment in a way that enhances growth, survival

or reproduction of a second, neighbouring species. According to some definitions, facilitation can be mutualistic, antagonistic or commensal. However, as in the study of mutualism, the research focus has been on defining mechanisms and outcomes of interspecific benefit.

Despite the common focus on beneficial effects, explorations of mutualism and facilitation have proceeded virtually independently. The two fields have different origins, and the focal research questions have differed markedly. Yet, much can be learned about each of these forms of beneficial interaction by considering what has already been learned about the other. My major focus here is on evolutionary origins, maintenance and dissolution of benefit. As I will discuss, studies on the evolution of facilitation have barely begun. This is in marked con-

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trast to an extensive body of knowledge about the evolution of mutualism.

I first briefly review the concepts of mutualism and facilitation, both with regard to their basic biology and to how they have been studied by ecologists and evolutionary biologists. My goal is to identify similarities and differences that might inform which aspects of the biology of these positive interactions are and are not parallel; more in-depth reviews can be found elsewhere (Callaway 2007; Bronstein & Holland 2008; Brooker *et al.* 2008; Stadler & Dixon 2008). I next review five questions whose study is shaping our understanding of how mutualisms evolve. I will then summarize the little we currently know about the evolution of facilitation, relating this body of knowledge to the same set of organizing questions and suggesting a number of testable hypotheses. Finally, I identify gaps in our understanding of facilitation, as well as patterns in the approaches used to study it, that currently impede progress in understanding evolutionary processes and patterns. None of these problems is insurmountable, however, and I argue that evolutionary studies of facilitation have an exciting future.

### The biology of mutualism and facilitation: what do we know and when did we learn it?

Ecology and evolutionary biology are young sciences, each having coalesced fairly recently from multiple, independent fields of study. For instance, plant physiological ecology, with strong links to agriculture, has an early history quite separate from that of animal physiological ecology, which is rooted in medical research (McIntosh 1985). Progress has occurred and will probably continue to flourish at the boundaries, where parallels between independently studied phenomena can be discovered and pursued. The boundary between the study of facilitation and mutualism may well be one such area.

Mutualisms are reciprocally positive interactions between pairs of species, whether the benefits are quantified in terms of fitness or population dynamics. Although some older discussions restrict the concept to interactions exhibiting specificity and a long evolutionary history, mutualism is now considered to subsume even transient interactions of small effect, so long as both partners experience a net positive effect (Bronstein 2001a; Bronstein & Holland 2008).

Observations that we can now associate with mutualism date back at least to the natural historians of ancient Greece. An idea that the harmony of society mirrored an underlying harmony of nature arose at that point and then persisted in the Western world throughout the Middle Ages. For example, plants were said to provide food for animals, which in turn decayed to fertilize the soil for plants. Belief in this well-ordered universe finally began to unravel during the upheavals of the Industrial Revolution. Ideas of competition and struggle as forces of progress came to pervade the political and economic analyses of the time, spurred by the work of Thomas Malthus. Even though much of his focus was on competition and struggle within and among species, Charles Darwin was probably one of the first to give substantial attention to mutualism. In showing that mutualisms could emerge in nature

strictly by selfish actions, limited by costs and driven by conflicts of interest between partners, *The Origin of Species* (Darwin 1859) laid much of the groundwork for current studies on the evolution of mutualism.

By the end of the 19th century, hundreds of articles had been published describing the natural history of various mutualisms. However, despite the wealth of available information, mutualism was not a prominent concept in ecology through most of the 20th century. Ecologists interested in species interactions focused almost exclusively on competition and predation, and did not explore the relationships and close links among different forms of interspecific interactions. The first major conceptual advances only began in the 1960s, and it is only since the mid-1980s that the field of mutualism has truly flourished.

The history of research on facilitation has proceeded along a different pathway. It is a comparatively young field and one that emerged out of a different historical background: Callaway (2007), Brooker *et al.* (2008) and others clearly identify its origins in 20th-century plant community ecology. The earliest research on facilitation focused on plant–plant interactions in which certain individuals experience higher performance in the presence of a neighbouring species. Thus, for example, Callaway (2007) identifies the first study of facilitation as an experiment conducted in 1914 by G.A. Pearson that demonstrated that conifers regenerated more successfully after fires when they grew within *Populus tremuloides* (quaking aspen) clones. Facilitation was also recognized early to be a potentially important mechanism of plant succession. Most research in this field continues to focus on plant–plant interactions. However, facilitation has also been identified among other groups of organisms, including those occupying different trophic levels. For example, Bracken, Gonzalez-Dorantes & Stachowicz (2007) have documented the role of invertebrates in facilitating the dominance of a foundation species, the green filamentous seaweed *Cladophora columbiana*, in rocky intertidal habitats. Importantly, the idea of facilitation emerged out of an interest in the role of competition in the structure and function of communities. Competition ultimately played little part in the development of mutualism as a field of study, despite Darwin's early recognition of its role.

Detailed conceptual consideration of facilitation began in the mid-1980s, around the same time when mutualism began to attract serious attention from a different set of ecologists. Furthermore, like mutualism (Bronstein 1994a), facilitation has had a slow entry into mainstream ecological thought (Bruno, Stachowicz & Bertness 2003). One difference, however, is that the study of mutualism had a few thousand years' head start in the accumulation of examples. By the time that a conceptual foundation began to develop, the range of benefits offered by mutualists, the kinds of organisms and environments in which mutualisms were common, most of the important traits, as well as the continuum from specialization to generalization were already well documented. Furthermore, biologists were already aware of the fundamental evolutionary questions posed by cooperation, although they had not yet investigated their answers.

One notable characteristic of the literature on facilitation is that the definition of the concept itself has been remarkably fluid. Unlike the extensive literature on the definition of mutualism, which began barely a decade after the term was first coined (Bronstein 2001a), this inconsistency has received little attention. Facilitation is sometimes defined as an interaction that benefits one species and does not harm the other (e.g. Bruno, Stachowicz & Bertness 2003); that is, it can be neutral or beneficial to the facilitating species, but not detrimental. In other definitions (e.g. Callaway 2007), facilitation can have any possible outcome (beneficial, neutral or even harmful) to the facilitator; the interaction is facilitative as long as the effect on the other species is positive. Some authors make overt or implied reference to the phenomenon specifically involving local effects (e.g. Verdú & Valiente-Banuet 2008) or organisms at the same trophic level only. Certain discussions of the concept exclude cases in which the partners directly interact, focusing on situations in which one species profits from how another alters the abiotic environment or in which resources are shared between species. Consequently, while an outstanding body of conceptual work and predictive theory has been developed in recent years, it is unlikely to pertain to the full range of interactions that are currently referred to as facilitative in the literature.

To achieve the goal of this study, viz., to identify evolutionary phenomena common to both mutualism and facilitation, it is critical to first define the similarities and differences between them. But to do this, we need clear and stable definitions of the scope of each concept. One could hypothesize two alternative relationships between mutualism and facilitation. Facilitation could be defined as all positive interactions, i.e. those that are beneficial for at least one partner; mutualism would then be the subset of those that are beneficial to both partners. Based on this view, any generalization, theoretical or empirical, regarding mutualism would be relevant to a subset of facilitation. Alternatively, one could consider only some mutualisms to also be cases of facilitation. This is the appropriate view if,

for example, local interactions among neighbours are considered to be a fundamental part of the definition of facilitation. In that case, certain mutualisms (notably pollination and seed dispersal, interactions that involve potentially long-distance movements across a landscape) would be excluded. This view would also be appropriate if one were to constrain facilitation to refer to positive relationships among individuals at the same trophic level, as most mutualisms cross trophic levels (Holland *et al.* 2005). I will subsequently assume this latter relationship between mutualism and facilitation (i.e. that some but not all mutualisms are cases of facilitation), while leaving somewhat vague the exact definitions of phenomena that occur within and outside the area of overlap. Table 1 provides the examples of interactions that, according to the scheme I have adopted, would be considered mutualistic only, facilitative only or both mutualistic and facilitative.

Exploring the precise relationship between mutualism and facilitation will thus require further attention to the scope of interactions that can be agreed upon to be facilitative. Three striking similarities nevertheless emerge when one contrasts the literature that has developed independently on each form of interaction. First, as can be seen in Table 1, there is a relatively short list of benefits that each of these interactions can confer. One of these is protection from stressful environmental conditions, whether stress is defined as biotic or abiotic. The best-understood examples of plant–plant facilitation involve a host individual that moderates the harsh abiotic conditions that would prevent another from persisting (Bertness & Callaway 1994; Brooker *et al.* 2008); one well-understood class of mutualisms involves a species that gains protection from the abiotic environment or natural enemies via association with a species at the same or different trophic level (Bronstein & Barbosa 2002; Redman *et al.* 2002; Hay *et al.* 2004). A second well-defined benefit involves the acquisition of limiting nutrients from a partner. In particular, plants' interactions with both mycorrhizal fungi and *Rhizobium* bacteria have been treated as examples of both facilitation and mutualism.

**Table 1.** Examples of interactions that could reasonably be classified as mutualistic only, facilitative only, or both mutualistic and facilitative

	Positive effect	Reference
Mutualism only		
Pollination	Exchange: transport of pollen between plants usually for food reward	1
Seed dispersal	Exchange: transport of seeds to suitable microhabitats for food reward	2
Mutualism and facilitation		
Ant protection	Exchange: protection from natural enemies usually for food reward	3, 4
Associational defense	Mutual protection of neighbours from natural enemies	5, 6
Shared mutualist attraction	Mutual attraction of pollinators and seed dispersers by neighbours	7, 8
Nutritional symbioses	Mutual exchange of limiting nutrients (usually)	9, 10
Associational growth (reciprocal)	Reciprocal improvement of habitat by neighbour (via moderation of stress, increased access to nutrients, etc.)	11
Facilitation only		
Associational growth (unilateral)	Unilateral improvement of habitat by neighbour (via moderation of stress, increased access to nutrients, etc.)	12, 13

References: 1, Pellmyr (2002); 2, Herrera (2002); 3, Stadler & Dixon (2008); 4, Rico-Gray & Oliveira (2007); 5, Hay *et al.* (2004); 6, Atsatt & O'Dowd (1979); 7, Moeller (2004); 8, von Zeipel & Eriksson (2007); 9, Smith & Read (2009); 10, Douglas (1994); 11, Pugnaire, Haase & Puigdefábregas (1996); 12, Callaway *et al.* (2004); 13, Greenlee & Callaway (1996).

A second feature shared by mutualism and facilitation is that costs and not only benefits usually accrue within the interaction. The costs of mutualism have been extensively documented and frequently measured; they include, for example, costs of locating, attracting and rewarding the partners that confer benefits (Bronstein 2001b). Competition among species within one of the two guilds of mutualists has the potential to reduce the success of the shared species, and this, too, must be considered a cost of the interaction. Costs of facilitation have received much less attention (but see Callaway 2007). Certainly the best-understood of them involve competition, in this case between the facilitated and facilitating species themselves. Nurse plants that facilitate growth of other species, for example, may have negative effects on them as well, most obviously due to competition for nutrients and water. In certain pairs of species, the costs outweigh the benefits, potentially leading to species-specificity of nurse plant relationships (Callaway 2007).

Finally, both mutualism and facilitation are often context-dependent or conditional interactions. That is, whether a pairwise association is beneficial, neutral or detrimental varies with the ecological setting in which it takes place. Studies documenting shifts between competitive and facilitative outcomes in plant–plant interactions along gradients of physical stress and consumer pressure (reviewed by Brooker *et al.* (2008)) are studies of context-dependency, although this term is not in common use in the facilitation literature (but see Callaway, Pennings & Richards 2003). Context-dependency has been extensively documented in mutualisms as well (Thompson 1988; Cushman & Addicott 1991; Bronstein 1994b). Well-studied context-dependent mutualists include insects that alternately pollinate and rob nectar from flowers (Irwin, Brody & Waser 2001), lycaenid larvae that only reward ants when they perceive natural enemies nearby (Leimar & Axén 1993) and mycorrhizal fungi that only benefit their host plants when soil nutrients are limiting (Johnson, Graham & Smith 1997). Shifts between mutualism and competition (e.g. Warner, Travis & Dunson 1993) appear to be rare, probably because few mutualisms involve species occupying the same trophic level. Rather, mutualisms grade into either commensal (+0) or antagonistic (+−) outcomes, as a function of nutrient availability (Jones & Smith 2004), abiotic conditions (Kersch & Fonseca 2005), the presence of other species (Bronstein & Barbosa 2002) and partner abundance (Theimer 2005). Only few of these studies have yet been conducted along ecological gradients (but see, e.g. Abbot *et al.* 2008), in contrast to the bulk of studies of this phenomenon in facilitative interactions.

Thus, clear ecological similarities can be recognized between mutualistic and facilitative interactions even in the absence of precise definitions. The most striking difference appears to be the close link between facilitation and competition, on the one hand, and mutualism and antagonism, on the other. The causes seem to be (i) the dominance of facilitation (or at least facilitation studies) among neighbouring organisms occupying the same trophic level, which share an often limiting pool of resources and (ii) the fact that most (or at least the best-studied) mutualisms are consumer–resource interactions in which

consumption has a beneficial rather than detrimental effect for the consumed (Holland *et al.* 2005).

## Evolution of mutualism and facilitation

Research on mutualism has been characterized by at least a passing interest in its evolution since Darwin pointed out in *The Origin of Species* the paradox of cooperation in the struggle for existence (“Natural selection cannot possibly produce any modification in a species exclusively for the good of another species; though throughout nature one species incessantly takes advantage of, and profits by, the structures of others...If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.” (Darwin 1859)). Early evolutionary biologists did not, however, deal with mutualism in any focused way. Their concern was with the genetic basis of individual traits, and they did not focus on any form of interspecific interaction until the middle of the 20th century. Soon afterward, several distinct lines of inquiry coalesced into the current intense interest in mutualism evolution. Studies investigating and measuring selection and diversification of individual traits began to focus on characters such as floral traits that served critical functions within mutualistic interactions. From another direction, a growing interest in co-evolution quickly broadened to include mutualisms. Simultaneously, theorists interested in how intraspecific cooperation can persist in the face of cheating and defection began to extend their ideas to the between-species context.

In contrast, few evolutionary aspects of facilitation have yet been explored. Brooker *et al.* (2008) point out that “although the possible relationships between facilitation and evolution have been discussed previously...an evolutionary focus is absent from almost all recent work in the facilitation field”. This is likely an outcome of facilitation’s origins in plant community ecology, a field that only recently has begun to explore evolutionary issues (Enquist *et al.* 2001). Most current evolutionary research on facilitation focuses on its role in niche construction (e.g. Valiente-Banuet *et al.* 2006), and evolutionary theory relevant to these interactions is still rare (but see, e.g. Brooker & Callaghan 1998; Kefi *et al.* 2008). The evolution of facilitative relationships themselves, the focus of this paper, remains minimally investigated.

Yet, there is no doubt that inquiries into the evolutionary origins and maintenance of facilitation would be illuminating. Have traits evolved that enhance species’ abilities to benefit from their neighbours and/or that enhance (or reduce) a species’ abilities to provide those benefits? What conditions favour specificity versus generalization within facilitative relationships? Do facilitators and facilitated species co-evolve?

One approach to studying the evolution of facilitation is to begin with the types of inquiries that, over the past several decades, have oriented investigations into the evolution of mutualism. From this basis, we can consider which of these lines of



research might be most interesting, important and feasible to pursue for this other form of positive interaction. Below, I present five questions regarding the evolution of mutualism, the approaches that have been used to explore them, and some of the most important answers that are currently emerging (see also Bronstein, Alarcón & Geber 2006). I then examine the same questions with regard to facilitation.

#### THE EVOLUTION OF MUTUALISM: ORIENTING QUESTIONS

##### *Evolution of mutualistic traits*

How do traits central to the functioning of mutualism, particularly attractants and rewards, arise and evolve?

The study of mutualism had its origin in organismal biology, and many of the traits that have been of greatest interest to organismal biologists have been those that serve some function within mutualisms. Particularly well investigated are plant traits involved in attracting and rewarding pollinators and seed dispersers. Selection experiments (e.g. Geber & Eckhart 2005), experimental manipulations (Internicola, Bernasconi & Gigord 2008) and phylogenetic studies (Herre, Jandér & Machado 2008) have been particularly informative for testing hypotheses on the origins and functions of these plant traits. The evolution of key traits of animal mutualists has received considerably less attention (but see, e.g. Oliver, Leather & Cook 2008). In part, this is because animal traits have been harder to manipulate, but also because in many mutualisms, evolution itself has been asymmetrical. This is particularly evident in mutualisms between mobile and sedentary species. Mobile partners such as pollinators and seed dispersers commonly forage and make choices that lie within a behavioural repertoire also used by their relatives not involved in mutualisms; sedentary partners such as plants have evolved suites of traits that take advantage of those behaviours for their own benefit (Bronstein, Alarcón & Geber 2006). Furthermore, many common mutualisms, including those involving invasive species, are unlikely to have undergone any evolution at all (O'Dowd, Green & Lake 2003).

##### *Specialization and generalization in mutualisms*

What conditions favour the evolution and maintenance of different degrees of specialization?

Remarkable variation in the specificity of association can be found within most forms of mutualism (e.g. Fleming, Venable & Herrera 1993; Hoeksema 1999; Ollerton 2006). With regard to plant partners, more specialized mutualisms generally involve the provision of rewards that are nutritionally more valuable as well as more protected from poorer mutualists. Specialization on the part of animals appears to involve dietary adaptations that permit relatively complete reliance on commodities that the plant partners provide. The degree of specificity within mutualistic networks is often strikingly asymmetric: one side of the interaction is considerably more specialized than the other, with the most special-

ized members of the network dependent upon a nested core of generalists (Bascompte & Jordano 2007). Guimarães *et al.* (2006) recently analysed dependence in several pollination, seed dispersal and ant-plant protection networks, and concluded that all show similar patterns of asymmetry and nestedness. Thompson (2005) and others contend that these similarities are likely due to the actions of similar evolutionary processes, such as convergence and complementarity among interacting species.

Phylogenetic studies indicate that evolutionary transitions between specialization and generalization are common in many mutualisms. The traits that have been under selection to produce such shifts are not yet well understood. In the case of ant-plant protection mutualisms, which range from highly specialized to loose and generalized, these transitions have involved gains and losses of only a few plant traits, primarily domatia (living space on the plant, such as swollen thorns) and elaiosomes (lipid-rich food bodies) (Heil & McKey 2003).

##### *Evolutionary origins and maintenance of mutualism*

How does mutualism arise? What conditions foster the evolution of mutualism, impede its evolution and lead it to break down?

This line of inquiry has emerged from two directions. First, an interest in the evolution of plant reproductive traits generated studies on transitions between abiotic and biotic (mutualistic) modes of pollination and seed dispersal. More recent studies have explored transitions towards and away from other mutualisms as well, including ant-plant and ant-Hemipteran protection, and nutritional interactions between plants and mycorrhizas and between leafcutter ants and fungi. This research has focused on costs and benefits of individual traits that function within mutualisms and the conditions that have apparently led to their gain and loss. Most recent work in this area has used phylogenetic approaches (Mueller *et al.* 2001; Lutzoni, Pagel & Reeb 2001; Shingleton & Stern 2003; Oliver, Leather & Cook 2008) that take advantage of information on trait distributions and biogeography. An unrelated research direction emerging from theoretical biology has focused on the paradox of cooperation in a fundamentally competitive and conflict-ridden world (Axelrod & Hamilton 1981; Sachs *et al.* 2004; Sachs & Simms 2006). Work in this area has used modelling approaches to explore the conditions under which mutualism is able to emerge and persist even in the presence of an apparent temptation to defect (Doebeli & Knowlton 1998; Ferrière *et al.* 2002; Foster & Wenseleers 2006).

Phylogenetic evidence is rapidly accumulating that the major forms of mutualism have been gained many times, judging from their very wide but scattered taxonomic distributions, biogeographical distributions and the diverse ontogenies of critical traits. These data suggest that mutualisms have been frequently lost as well (Sachs & Simms 2006). There is limited evidence at present that mutualisms are fundamentally unstable interactions, or that the evolutionary breakdown of mutualisms leads to species extinction.

### Co-evolution of mutualism

When are mutualists likely to co-evolve? What factors foster and impede these processes?

Reciprocal evolutionary change in interacting species, or co-evolution, was first identified and studied in plant–pathogen and plant–herbivore interactions (Thompson 1989). Co-evolution had entered the study of mutualism by the mid-1960s (Janzen 1966). Mutualism has since become one of the most thoroughly investigated interactions from the co-evolutionary perspective. Early attention focused on delineating the conditions under which mutualisms might co-evolve and the criteria for distinguishing co-evolution from other processes (e.g. Janzen 1980). More recently the focus has shifted towards studying putatively co-evolved interactions from a spatial perspective and identifying geographic variation that results from locally varying selection regimes (i.e. the geographic mosaic of co-evolution; Thompson 2005). Research has been both experimental and observational in nature (e.g. Thompson & Fernandez 2006; Heath & Tiffin 2007), with a strong genetic focus. Attention has also been given to identifying the subset of co-evolved interactions that show phylogenetic evidence of parallel cladogenesis, or co-speciation.

Many mutualisms, particularly those with some degree of specificity and obligacy, are now believed to show legacies of co-evolution. Co-evolution has been demonstrated to be a local process that can result in striking differences in traits and outcomes across the geographical range of a given interaction. On the other hand, many mutualisms, including but not restricted to highly generalized ones, show little evidence of a co-evolutionary history; traits of only one partner, or neither, have evolved in the context of the observed interactions. Reciprocal evolutionary change can only be detected when both partners are examined. Studies of mutualism are most often unilateral (Bronstein 1994a), and this alone may account for the lack of more evidence for co-evolution. However, asymmetric selection pressures are also quite likely. As pointed out above, mobile foraging partners whose activities are mutualistic commonly exhibit behaviours no different from their non-mutualistic relatives; their suite of behaviours have been co-opted by their partners for mutualistic ends, rather than having evolved in the context of that interaction.

### Cheating in mutualism

How commonly are mutualisms exploited by cheaters? How can mutualism persist evolutionarily in the face of cheating?

Organisms able to obtain the rewards and services that mutualists provide, while providing nothing to their partners in return, are extremely common (Bronstein 2001c; Yu 2001). These can be genetically distinct individuals within mutualistic species, individuals that exhibit context-dependent mutualistic and cheating behaviours, as well as species that act as interlopers on mutualisms that do not involve them. Particularly well-studied cheaters include nectar robbers (Irwin, Brody & Waser 2001), rhizobial bacteria that provide little nitrogen to their

hosts (Sachs & Simms 2008) and ants that fail to defend plants while monopolizing resources offered to mutualists (Gaume, Zacharias & Borges 2005). Natural history observations of cheaters extend back to the earliest studies of mutualism; focused interest in their effects on the evolution and stability of mutualism has emerged more recently, in the context of how cooperation in general can be stable in the face of the ‘temptation to defect’ (Bergstrom *et al.* 2003; Bronstein 2003; Sachs *et al.* 2004).

Traits have been identified that either prevent cheating or reduce its negative effects in several mutualisms (e.g. Pellmyr & Huth 1994; Kiers *et al.* 2003; Johnson, Hargreaves & Brown 2006; Nicklen & Wagner 2006). However, such traits are not as common as one might assume from theoretical analyses (Bronstein 2001c). It is possible that cheaters routinely overcome mutualists’ defences against them. Alternatively, the cost of being cheated, and the benefit of adopting a cheating strategy, may simply not be very high in most mutualisms. New models suggest that even when cheaters inflict a high cost, mutualisms are able to persist evolutionarily, although they may evolve differently in the cheaters’ presence than they would without them (Ferrière, Gauduchon & Bronstein 2007).

### THE EVOLUTION OF FACILITATION: CURRENT KNOWLEDGE, INTERESTING POSSIBILITIES AND MISSING DATA

#### Evolution of facilitation traits

Traits that characterize effective facilitator species are well known, at least for certain forms of facilitation. Traits allowing plants to harbour and reward soil microbial mutualists benefit those plants and lead, secondarily, to enrichment of the soil in certain limiting nutrients; thus, these plants facilitate the establishment of species that lack those symbionts (e.g. Callaway *et al.* 2004). Species with canopies that cast more shade on hot soils may be particularly effective nurse plants (Gómez-Aparicio, Valladares & Zamora 2006), and those that offer rich nectar rewards to pollinators are those most likely to facilitate pollination of neighbouring species (Laverly 1992).

In all of these cases, the traits in question clearly benefit the trait bearer (i.e. the facilitator) first and foremost. A reasonable hypothesis is that their effects on facilitated species are incidental byproducts of selection in another context. However, this is not necessarily the case. Many mutualistic traits, including specialized plant rewards and animal foraging behaviours, are similarly thought to have had their origins in other functions, and only been co-opted secondarily in the context of the positive interaction. Subsequently, however, they can be subject to selection and evolutionary modification (Leimar & Connor 2003). The critical question is whether species that are effective facilitators have undergone selection on key traits different from the selection regime on those same traits in species that are not effective facilitators. Answering this question would draw upon three sources of information: identification of key traits underlying facilitation, knowledge of the genetic basis of those traits, and identification of species or populations

possessing those traits that do and do not act as facilitators. At this point, sufficient information may be available only with regard to the first point.

Perhaps more expected would be the evolution of traits that increase performance of species able to use their neighbours towards beneficial ends. Selection may well favour facilitators able to *escape* from this relationship, if facilitation has any costs (see below). However, selection should strongly favour traits allowing organisms to *gain benefits* from their neighbours. Traits of facilitated species seem to have attracted significantly less attention than traits of facilitators. It would be extremely interesting to identify genetically based key traits of facilitated species, then compare those traits between species or populations that do and do not receive benefits from neighbours. For example, finding evidence that floral attractants differ between plant populations that historically have occurred in association with facilitators (i.e. neighbours known to jointly attract pollinators) and populations that have not would permit a test of the hypothesis that evolution can shape traits of facilitated species.

It should be pointed out that 'benefit' has been defined and measured inconsistently in studies of facilitation. Improved growth when in association with a neighbour, or the non-random association of species, can be highly informative for addressing most questions in the field. However, for evolutionary studies, it is ultimately necessary to measure fitness of the partners. It is also necessary to have fitness measures for individuals that do not engage in facilitation, as fitness is a relative concept. When there is no such variation, it becomes problematic to quantify benefits (Douglas & Smith 1989).

#### *Specialization and generalization in facilitative interactions*

Like mutualism, facilitation ranges from relatively specific to highly generalized. The set of mechanisms that can lead to specialization has been considered in some depth (Callaway 1998, 2007). Benefits may only be conferred by individuals that exhibit certain morphological traits, architectures or sizes, or that change their environments in specific ways. For example, plants may benefit from associating with neighbours that have particularly effective traits for deterring shared herbivores (Attatt & O'Dowd 1979) or for attracting and rewarding shared pollinators (Feldman, Morris & Wilson 2004). As a consequence, facilitated species may be non-randomly associated with potential facilitators. This phenomenon has been particularly well documented in certain nurse plant relationships (e.g. McAuliffe 1986; Greenlee & Callaway 1996). Conversely, only certain species might exhibit traits allowing them to reap the benefits that a potential facilitator can provide. Considerably less attention has been paid to this side of specialization.

What are the evolutionary causes and consequences of these ecological phenomena? Little is yet known. Two of the most general conclusions regarding the evolution of specialization in mutualistic interactions are that evolutionary transitions between specificity and generalization are frequent, and that the degree of specificity tends towards asymmetry between

partner species. It would be fruitful to explore whether the same patterns exist for facilitation. Such investigations, however, require (i) data on the phylogenetic distribution of facilitation and its specificity and (ii) reciprocal rather than unilateral studies of facilitation. Such data barely exist yet. Phylogenetic work on facilitation is in its infancy. Given the prominent role of phylogenetic studies in exploring the evolution of mutualism, it is clear that more such work is needed on facilitation if central evolutionary questions are to be addressed successfully. With regard to the second point, while benefits to facilitated species have been explored in depth in recent years, costs and benefits to the facilitator have been almost entirely overlooked (but see, e.g. Pugnaire, Haase & Puigdefàbregas 1996). Without such reciprocal studies, examining the symmetry of specialization and its evolutionary consequences is not possible. Nor are most other investigations of the evolutionary dynamics of facilitation.

#### *Evolutionary origins and maintenance of facilitation*

There has been minimal consideration to date of how facilitative interactions arise either *de novo* or in transition from other forms of interaction. Nor, to my knowledge, have the conditions that favour their evolutionary persistence or that lead them to break down been considered. However, reasonable evolutionary scenarios can readily be hypothesized. For example, an original state can be visualized in which individuals of two species grow intermixed. One of these (Species 1) alters the environment (e.g. by enriching its habitat with a limiting nutrient or by increasing the local abundance of a shared mutualist) in a way that is beneficial to the other. Imagine that individuals of Species 2 exhibit genetic variation in a trait that either makes them more likely to become established near Species 1 or more likely to take advantage of the altered environmental conditions. That trait would be expected to spread in the population, leading to the evolution of facilitation.

In this scenario, facilitation originates via evolution in the facilitated species, not the facilitator. That is, facilitation can be hypothesized to have a unilateral origin, except in cases where it is reciprocally beneficial. In that case, evolutionary change favouring the interaction might be expected to be bilateral. This observation emphasizes a central point: how facilitation will evolve should depend critically on the costs and benefits to both partners in the interaction, not simply to the facilitated species. In cases where the facilitating species (Species 1, in the above example) is neither benefited nor harmed by the species receiving benefit (Species 2), selection should not operate on that species in the context of the interaction. Thus, we can predict that facilitative interactions that would be classified as commensal should be evolutionarily stable, as should facilitative interactions that are mutualistic. Conversely, if costs to the facilitating species outweigh the benefits, i.e. if facilitation is antagonistic, a quite different outcome can be envisioned. If there is genetic variation for traits that might sever the association with the facilitated species (e.g. for the ability to exclude them as neighbours, or to diverge from them in shared characteristics), these should be favoured by natural

selection to the detriment of the partner. Alternatively, if there is no such genetic variation and if facilitation is sufficiently costly, the facilitator might ultimately be driven to extinction. Both of these processes are routes to the dissolution of facilitation, parallel to routes hypothesized to lead to the dissolution of mutualism (Sachs & Simms 2006). Thus, facilitation with either mutualistic or commensal outcomes can be predicted to show greater evolutionary stability than those with antagonistic outcomes. As in the case of mutualism, facilitation should have multiple origins, and should undergo frequent transitions back and forth to an absence of association.

Two significant gaps in the facilitation literature, both emphasized above, make these predictions difficult to test at present (though the verbal argument I present above can and should be subject to more rigorous theoretical exploration). First, comparatively few studies have focused on facilitated species and their traits (as opposed to facilitators and their traits); the genetic bases of those traits, if any, largely remain to be explored. Secondly, facilitation tends to be investigated in a unilateral fashion. In fact, as I have pointed out, it has been debated whether all of the above outcomes (mutualism, commensalism and antagonism) should even be considered as facilitation. Further progress in understanding the evolutionary origins and maintenance of facilitation must thus await studies that take an explicitly reciprocal approach.

#### *Co-evolution of facilitative interactions*

Not surprisingly, the lack of attention to reciprocal effects has led to a dearth of information on co-evolution. The arguments above, however, generate some predictions about the form of co-evolution that would be expected when relevant genetic variation exists in both partner species and when selection is strong and consistent enough to result in evolutionary change. In mutualistic facilitative interactions, co-evolution (if it occurs) should proceed as in mutualisms, with traits favoured that reinforce the benefits of the interaction while reducing its costs to both partners. In commensal facilitation, co-evolution would not be expected: evolution should proceed unilaterally in the facilitated species. Finally, in antagonistic facilitation, at least two co-evolutionary routes can be envisioned (see also Brooker *et al.* 2008). First, the facilitator might experience selection for traits that increase its tolerance to the partner's actions. This route can lead away from antagonism and towards a commensal outcome of facilitation, potentially increasing its evolutionary stability. Alternatively, there is the intriguing possibility of a co-evolutionary race. In this case, traits in the facilitated species that reinforce the association or that increase its ability to gain advantage from its partner would be favoured, while the facilitator would be under selection to escape (by evolving defences or sanctions against its exploiter, for instance). A similar pair of evolutionary routes is well studied in plant–herbivore interactions (Stowe *et al.* 2000).

There is every reason to expect that co-evolution of facilitative interactions, if it occurs, will take place in the kind of geographic mosaic pattern that is now well documented for mutualism. One of the best-documented features of facilitation

is variation in outcome from facilitation to competition along environmental gradients (reviewed by Brooker *et al.* 2008). Thus, selection can be expected to favour facilitation under predictable sets of conditions. It is likely that co-evolutionary models in which interaction outcomes are mutualistic only at some times and places (Nuismer, Thompson & Gomulkiewicz 1999, Nuismer, Thompson & Gomulkiewicz 2000, Gomulkiewicz, Nuismer & Thompson 2003; Nuismer, Gomulkiewicz & Morgan 2003) could profitably be extended to facilitation as well. Theoretical work in this area is under way (Travis, Brooker & Dytham 2005, Travis *et al.* 2006).

#### *Cheating in facilitation*

While cheating is clearly ubiquitous in mutualism, its existence in facilitative interactions is essentially unknown. Cheating arises when there is a cost to participating in a positive interaction; under those conditions, evolution can favour individuals able to reap benefits from a partner while avoiding this cost. Cheating in facilitation would thus involve avoidance of investments necessary to receive benefits from a facilitator. Do facilitated species make such investments, and if so, is there genetic variation for them? Further research on these species' traits will be required before this question can be addressed.

Although it has not previously been identified as such, one of the best-studied forms of cheating may in fact involve facilitation. Müllerian or mutualistic mimicry complexes involve shared defence by unpalatable species (Elias *et al.* 2008) and shared attraction of mutualists (Raguso *et al.* 2003). As these effects only occur among neighbours that share antagonists or mutualists, they might reasonably be considered examples of facilitation. In a number of these systems, additional species (sometimes termed Batesian mimics) gain the benefit of defence without investing in unpalatability (Ritland 1994) or rewards (Internicola *et al.* 2007). Should these be considered cheaters on facilitative interactions? Or are Batesian mimics engaged in facilitation themselves (since they gain benefit from neighbour species, albeit at a cost to them)? The answer depends upon whether one adopts a definition of facilitation that subsumes antagonistic as well as benign and positive outcomes.

#### **Conclusions**

Three main conclusions emerge from the arguments I have presented here.

First, moving towards a unified understanding of the evolution of facilitation awaits a clarification of the scope of the concept. Certain evolutionary issues are likely to be of little relevance to facilitation if, for example, the concept is defined to include only partners occupying the same trophic level, only phenomena that take place between neighbours or only interactions with non-negative outcomes. Conversely, if the concept is defined too broadly, such that it includes any kind of interaction involving positive outcomes for at least one species, then facilitation risks being little more than a grab-bag of diverse



phenomena, each with unique ecological and evolutionary features. In that case, little can be gained from considering 'evolution of facilitation' as a distinct field of inquiry, with a set of orienting principles, patterns and hypotheses. The challenge is to identify features, both ecological and evolutionary, that unite diverse kinds of facilitation. The field of mutualism is taking on this same challenge (e.g. Boucher 1985; Bronstein 1994a; Herre *et al.* 1999; Sachs *et al.* 2004; Holland *et al.* 2005; Foster & Wenseleers 2006).

Secondly, studies on the evolution of facilitation are at a very early stage, but the future is exciting. Enough is known about traits involved in facilitation and the range of specificity of these associations so that reasonable hypotheses can be offered with regard to diverse evolutionary issues. Using current research on the evolution of mutualism as a guide, I have identified five key questions that might orient future research: How do key traits evolve within facilitative interactions? What forces favour the evolution of specialization? What are the forces that favour the evolution of facilitation and that lead to its evolutionary dissolution? Under what conditions will facilitative interactions co-evolve, and how will this occur? Finally, are facilitative interactions exploited by cheaters, and if so, what are the evolutionary consequences for facilitation? I have suggested a number of testable hypotheses in relation to each of these questions. More and better ones will undoubtedly emerge as studies begin to accumulate.

The final conclusion relates to the challenges involved with actually testing these evolutionary hypotheses. As I have emphasized throughout, the study of facilitation has historically rested within community ecology, and its classic orienting questions are quite different from those posed here. As a consequence, for these evolutionary questions to be tackled successfully, facilitation will need to be studied somewhat differently than at present. First, it will be essential to take a bilateral approach. It is reasonable to suppose that facilitation evolves like mutualism when it is reciprocally beneficial, like commensalism when the facilitator is neither benefited nor harmed, and like parasitism, herbivory or other antagonistic interactions when it exacts a fitness cost on the facilitator. Secondly, the genetic basis of traits involved in facilitation will need to be explored, as well as the degree of variation in those traits. Selection cannot act, of course, if traits either lack a genetic basis or do not vary. In particular, attention will need to be paid to traits of the species that receive the benefits of facilitation. Finally, we will need to know much more about fitness costs and benefits. Only then will it be possible to identify conditions under which selection is likely to favour the evolution and persistence of these interactions.

Many more questions could be asked about the evolution of facilitation than the ones discussed here. Research on some of them is already under way. For example, data and models are suggesting that facilitation can increase the evolutionary persistence of species and can act as a force that shapes species' niches (Valiente-Banuet *et al.* 2006; Kefi *et al.* 2008). Future work on these issues, as well as the ones I have discussed here, have the potential to lead to deeper understanding of population- and community-level processes, and to highlight even

more strongly the role of positive interactions in the history of life on Earth.

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