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SPECIAL FEATURE

FACILITATION IN PLANT COMMUNITIES

A multitrophic perspective on functioning and evolution of facilitation in plant communities

Wim H. van der Putten*

Netherlands Institute of Ecology, PO Box 40, 6666 ZG Heteren; and Laboratory of Nematology, Wageningen University and Research Centre, PO Box 8123, 6700 ES Wageningen, The Netherlands

Summary

1. Plant facilitation has been studied mostly in the context of plant–plant interactions, whereas multitrophic interactions including those that occur below ground have not yet received much attention. Here, I will discuss how above-ground and below-ground natural enemies and their predators influence plant facilitation and its evolution.

2. Specific above-ground and below-ground plant enemies and their predators play a major role in structuring the composition and dynamics of plant communities. In successional sequences, above-ground and below-ground multitrophic level interactions may tip the balance from competitive to facilitative states and vice versa.

3. Little is known about how above-ground and below-ground multitrophic interactions develop along resource or stress gradients and how the outcomes of above-ground–below-ground interactions depend on variations in these environmental conditions.

4. Facilitated plants need to fit into the above-ground–below-ground multitrophic communities of their facilitators.

5. Little is known also about the evolution of plant facilitation. The observed distance in phylogeny between facilitators and facilitated plants suggests that host-specific enemies may very well co-determine which species become facilitated by which facilitators.

6. Further, very little attention has been given to how plant strategies (allelopathy, accumulation of enemies, monopolization of symbionts) may be the result of selection against being facilitative.

7. *Synthesis*. Plant facilitation cannot be understood without considering a plant's natural enemies and also its enemies' enemies. Plant enemies can turn competitive interactions into facilitative interactions, whereas the enemies' enemies can turn facilitation back into competition. Below-ground interactions will have longer-lasting effects on facilitation than those above ground, because many organisms can persist in the soil, even when the host plants have disappeared.

Key-words: above-ground, below-ground, competition, direct and indirect defence, direct and indirect facilitation, mycorrhizal fungi, natural enemies, plant facilitation, plant traits, predators, selection

Introduction

The concept of facilitation is based on the principle that individuals influence their environment at the benefit of their own offspring or of other species. The importance of facilitative processes has been overlooked due to the overwhelming interest for competitive or antagonistic interactions (Connell & Slatyer 1977; Bertness & Callaway 1994). Currently, there is increasing interest in facilitation, especially in indirect interactions (Brooker *et al*. 2008). Indirect interactions may include interactions with a third plant species, but they may also include interactions with the enemies or the enemies of the enemies (Wootton 1994).

A number of reports have shown that plant facilitation is affected indirectly by above-ground vertebrate herbivores (Smit, Den Ouden & Müller-Schärer 2006; Smit *et al*. 2007). Besides vertebrates, invertebrate herbivores and microbial pathogens, both above ground and below ground, play important roles in shaping plant–plant interactions (Wardle *et al*. 2004). Together, plants, their enemies, symbionts and their predators interact in above-ground–below-ground multitrophic food webs, which influence the ecology and evolution of plant

*Correspondence author. E-mail: w.vanderputten@nioo.knaw.nl

traits, defensive strategies and life-history strategies (Van der Putten *et al.* 2001). Here, I will discuss the role of invertebrate herbivores and microbial pathogens, both above ground and below ground, as well as their predators, and discuss how their consideration may further develop our understanding of plant facilitation along resource and stress gradients.

Direct facilitation involves protection against adverse abiotic environmental conditions such as drought, intensive radiation or turbulence. Facilitation between two species is considered to be indirect when it is modified by a third species (or more), therefore only occurring when more than two species are present (Brooker *et al.* 2008). This is where definitions may become problematic, as there are many types of indirect effects in facilitative interactions, including other species of the same or different trophic levels (Wootton 1994). For example, facilitation is considered to be indirect when facilitators allow other species to hide from their natural enemies (Stachowicz 2001). Otherwise, unpalatable plants may facilitate palatable plants by protecting them against above-ground herbivores (Smit, Den Ouden & Müller-Schärer 2006).

In my view, indirect plant facilitation can be due to other plants, the build-up of symbioses, natural enemies, or trophic networks that include decomposer organisms and carnivores as well. These interactions can take place above ground, below ground or in both subsystems at the same time; above-ground interactions can be influenced by below-ground interactions vice versa, often involving complex plant chemistry (Van der Putten *et al.* 2001; Bezemer & van Dam 2005). In that sense, facilitation by plant protection against herbivores (Smit, Den Ouden & Müller-Schärer 2006; Smit *et al.* 2007) could be called indirect, although it may be that when herbivores are excluded the palatable plants still are benefiting from early development inside pockets of unpalatable plants, simply because they are adapted to, for example, germination under conditions of moisture and shade.

Little is known about how these complex direct and indirect interactions in multitrophic communities work out along environmental gradients, such as from low to high resource levels, or from high to low stress levels. To some extent, low-resource conditions may correlate with high-stress conditions, but this is not necessarily the case. For example, in tidal brackish water estuaries, resource levels can be fairly high due to nutrient inputs by detritus (Van Wesenbeeck *et al.* 2007), whereas stress due to wave action can be high as well. In most of my examples, I will focus on resource gradients. I will first explore if there are emerging properties of indirect facilitation due to multitrophic interactions that may lead to general predictions. Then, I will explore how facilitative interactions may evolve over time and how this evolution may depend on ecosystem properties (Price 1984).

Why do above-ground and below-ground interactions need to be considered specifically? This is a fundamental question and involves the question to what extent soil organisms differ from species that complete their life cycle above ground? Clearly, below-ground interactions have different spatial and temporal dimensions than interactions above ground (Bardgett *et al.* 2005; De Deyn & Van der Putten 2005). Above-ground herbivores or pathogens may disappear soon after their host plants have vanished. Below-ground biotic interactions cause changes in the system properties, such as the accumulation of organic matter, alteration of organic matter quality or the survival of soil organisms as spores or cysts. These changes below ground may cause legacy effects lasting longer than those above ground. For example, work on replant diseases in orchards has shown that pathogen accumulation effects of previous tree stands may last for years or even decades, preventing the re-establishment of the same tree species unless the soil is being sterilized (Hoestra 1968). Such long-lasting effects are typical of soil and less of above-ground subsystems and I will provide some examples suggesting that this affects plant–plant facilitation as well.

Because below-ground interactions have longer-lasting legacy effects than above-ground interactions, due to the survival of many soil microbes after the host plants have disappeared, above-ground principles cannot be immediately translated as predictions of what may happen below ground. Moreover, most organic material is decomposed on the soil surface or in the soil providing the soil with a different role in resource acquisition, namely of converting organic materials into mineral nutrients. For example, under trees seedlings may be facilitated by hydraulic lift or by nutrients from decomposing organic matter, whereas above-ground sunlight necessary for photosynthesis could be a limiting factor under shade. Therefore, both above-ground and below-ground subsystems play an important role in facilitation, but their effects can point into opposite directions and their span of action could develop along different time horizons.

Facilitation along resource gradients

Plant traits and plant community properties vary greatly along resource gradients. At the low end of resource supply, plants grow slowly and strongly defend their acquired nutrients by toxic compounds. At the high end of resource supply, plants grow fast and invest less in defending their tissues by toxic compounds. Therefore, along gradients from low to high resource supply, trade-offs are to be expected between defence at low resource levels to growth at high resource levels (Herms & Mattson 1992; De Jong 1995), although these generalities do not account for all observed variation in plant defence strategies (Hamilton *et al.* 2001; Stamp 2003). This and other trade-offs will have consequences for the patterns in plant facilitation; unpalatable or thorny plants may facilitate palatable plants with well-edible tissues, but when herbivores are directed away from the facilitators towards the facilitated plants, the facilitated plants may be over-exploited by herbivory. Moreover, thorns may work against large herbivores, but their effectiveness against above-ground invertebrate herbivores or pathogens can be less, whereas below-ground enemies may be not affected at all.

Little is known about such trade-offs between defence and growth along stress gradients. High-stress environments may occur in, for example, coastal dunes, where waves and sand movement cause erosion or unpredictable burial (Maun 1998).

However, these environments are also relatively poor in nutrients, so that here the resource and stress gradients are, at least to some extent, correlated. Probably, in systems where high stress is not correlated with low resource supply, such as in estuarine marshes, the role of facilitation can be less well related to plant defensive and growth strategies, as grazing might prevent outgrowth of emergent aquatic plants under stressful conditions.

Succession gradients produce excellent opportunities for examining how indirect facilitative interactions may vary with abiotic and biotic changes in the environment and the emerging plant life histories. Probably, these comparisons are standing a bit further away from most current cases of plant facilitation, but they nicely show the complexity of biotic and abiotic interactions, that may as well take place in other systems. For example, in temperate dunes of the northern hemisphere, one of the earliest pioneer species is *Ammophila arenaria* (marram grass). This grass tolerates salt spray as well as sand burial by 1.20 m per year (Huiskes 1979), and it is in symbiosis with arbuscular mycorrhizal fungi (Kowalchuk, Gerards & Woldendorp 1997). Due to these traits, the grass is responsible for natural dune building and sand stabilization under extremely nutrient-poor and low-water conditions. By doing so, *A. arenaria* facilitates for plant species of later successional stages, as the successors cannot colonize the original harsh environment of the beach. However, when building and stabilizing dunes, *A. arenaria* is a strong competitor because it accumulates so much wind-blown sand that no other plant can survive those conditions (Huiskes 1979).

The inhibitory effect of *A. arenaria* is only broken when sand deposition diminishes, for example at the leeward side of dunes, or when new dunes are formed on the beach, which block the transport of drift sand to the existing dunes. Then, *A. arenaria* plants degenerate and become replaced by other grasses, the sedge *Carex arenaria* and the nitrogen-fixing shrub *Hipphophaë rhamnoides* (Oremus & Otten 1981). Many researchers have considered possible reasons for this *Ammophila* decline in stabilized dunes (Little & Maun 1996), including nutrient limitation (Willis 1965; Hope-Simpson & Jefferies 1966), ontogeny (Marshall 1965), competition (Huiskes 1979), lack of free-living or symbiotic mutualists (Hassouna & Wareing 1964; Nicolson & Johnston 1979) and overwhelming by soil pathogens (Van der Putten, Van Dijk & Troelstra 1988).

The soil pathogens that contribute to the *Ammophila* decline do not harm later succession plant species, because species like *Festuca rubra* ssp. *arenaria*, *C. arenaria* and *Elymus athericus* are tolerant of the pathogens of *Ammophila* (Van der Putten, Van Dijk & Peters 1993). This tolerance provides the later succession plants with an advantage in interspecific competition. Without the soil pathogens *A. arenaria* and *F. rubra* are equally competitive, but in the presence of the soil pathogens *A. arenaria* is outcompeted by *F. rubra* (Van der Putten & Peters 1997). Therefore, the soil pathogens of *A. arenaria* indirectly contribute to the replacement of *A. arenaria* in dunes.

Later succession plant species are not as tolerant to salt spray and sand deposition (Huiskes 1979; Sykes & Wilson 1988, 1990) as *A. arenaria* is. Thus, later succession plants benefit from the sand-stabilization and dune-building activity of *A. arenaria*. However, without soil pathogens, the facilitator *A. arenaria* would be far less easily replaced by later succession plants than when it is exposed to soil pathogens (Eppinga *et al.* 2006). Therefore, the soil pathogens of *A. arenaria* facilitate the later succession plant species by weakening the competitive ability of *A. arenaria*.

The soil pathogens are already present in the root zone of vigorous *A. arenaria*. Both the plant and the pathogens move up through the wind-deposited sand layers throughout the growing season. Therefore, yearly sand deposition and emergence of the plants from sand burial is a prerequisite for remaining vigorous (Van der Stoel, Van der Putten & Duyts 2002). This dune system has become a model of how soil pathogens may influence plant performance and plant replacement; it probably also serves as an example of how soil pathogens can contribute indirectly to plant facilitation. Not all researchers working in this area will consider these temporal sequences as facilitation, but in a way they are, and the same processes probably take place in many other systems, but then at smaller spatial and temporal scales.

Secondary succession on old fields represents another resource gradient, but this time the reverse of that in coastal foredunes. Early-abandoned fields are relatively rich in nutrients and the abundance of early succession weeds results in canopies that make light a limiting resource. Therefore, in secondary succession trade-off patterns between growth and defence would be expected to be reversed when compared with primary succession; early secondary succession plants should invest more in growth and later secondary succession plants should invest more in defence. However, field studies show less clear patterns than theory predicts. Within successional stages, plant species differ in their susceptibility to herbivores and pathogens, whereas along successional gradients effects of above-ground biotic interactions may differ from those below ground. In general, in grasslands above-ground and below-ground herbivores and pathogens may enhance, or slow down, plant species replacement (Brown & Gange 1992; Hulme 1996; De Deyn *et al.* 2003; Schädler *et al.* 2004; Kardol, Bezemer & van der Putten 2006), Above-ground herbivores would facilitate early secondary succession plant species, whereas below-ground herbivores and pathogens would facilitate later secondary succession plant species.

In conclusion, indirect facilitation operates both in primary succession in coastal foredunes and in secondary succession following abandonment of arable or grassland fields. The outcome of indirect facilitation depends strongly on whether the enemies are acting above ground or below ground and whether they act against the earlier or the later succession plant species. If above-ground or below-ground herbivores slow down succession, they facilitate early succession plant species at the expense of later succession species. Otherwise, when they enhance the rate of succession, later succession plant species will be indirectly facilitated at the expense of early succession plant species.

These examples of facilitative processes along successional sequences may not be considered 'immediate and on the spot' facilitation as facilitative processes are usually considered to be in current facilitation studies. However, in the classic literature on succession these processes have been named ‘facilitation’ as well. Moreover, the studies on successional sequences nicely show how above-ground or below-ground enemies can play a role in plant–plant interactions and plant community development. They also show that effects of above-ground and below-ground herbivores and pathogens do not necessarily work out into the same direction of succession. Moreover, as many soil pathogens can remain in the soil due to survival structures, their accumulation may result in long-lasting historical legacy effects, which determine, for example, the length of the crop rotation cycle in agriculture and the directionality versus cycles in composition changes in natural plant communities.

Facilitation from a multitrophic perspective

Thus far, the role of herbivores and pathogens in facilitation has been considered without including the enemies of the plant enemies. Moreover, facilitation during succession also involves changes in the abiotic conditions of the ecosystem. Here, facilitation will be discussed from the perspective that plants are part of multitrophic communities, interacting with their facilitators.

According to the Janzen–Connell hypothesis (Janzen 1970; Connell 1978), young individuals cannot establish close to mature individuals that carry a high enemy load to which the young individuals are sensitive. Therefore, this hypothesis would predict that facilitated plants will be tolerant of, or resistant to, the enemies of their facilitators. This hypothesis would also predict that young individuals might make use of the predators of the enemies of the facilitators to control their own enemies (Fig. 1). The Janzen–Connell hypothesis has been developed for low-land tropical rain forests and coral reefs, however, it also applies to, for example, temperate forest (Packer & Clay 2000). Janzen–Connell processes enhance the likelihood that plants can only facilitate heterospecifics that are tolerant of, or resistant to, the enemies of their facilitator, or conspecific plants that may benefit from the defence systems of their conspecifics.

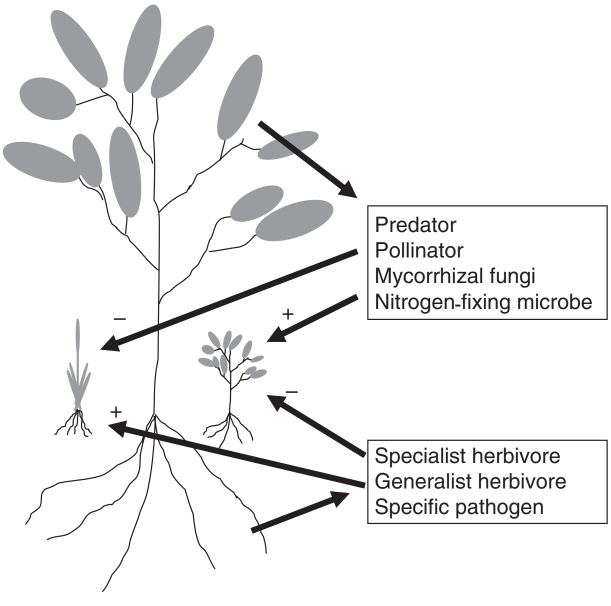

Fig. 1. Conspecific (small plant right) and heterospecific (small plant left) plant facilitation from a multitrophic perspective.

In coastal dunes, later successional plant species indeed are tolerant of the soil pathogens of their predecessors (Van der Putten, Van Dijk & Peters 1993). In secondary succession gradients, mid-succession grasses received negative feedback from early-succession grasses (Kardol *et al.* 2007), so that early-succession grasses provided mid-successional forbs with an indirect advantage over mid-successional grasses. Therefore, in those succession gradients inhibition and facilitation seem to be two sides of a coin, and the accumulation of natural enemies, or of predators, may make the coin flip to one side or the other. A challenge for community ecologists would be to re-analyse plant community interaction patterns from such a multitrophic perspective. Possibly, patterns of facilitation, trait combinations and relatedness between facilitators and facilitated plant species may find their origin at least to some extent in multitrophic Janzen–Connell processes.

Plants defend themselves against natural enemies in a variety of possible ways: by avoidance, tolerance, or direct or indirect defence (Karban & Baldwin 1997; Strauss & Agrawal 1999). The defences can be physical or chemical and they can be constitutive or induced upon attack. Indirect defence involves the enemies of the plant’s attackers, which can be attracted by release of attractive cues, such as volatiles (Vet & Dicke 1992) or sugars (Wäckers, van Rijn & Heimpel 2008). Plant defence has been studied mostly from an above ground and tri-trophic perspective, but recent studies have shown that above-ground trophic interactions can permeate through five trophic levels (Harvey, Wagenaar & Bezemer 2009). Moreover, an increasing number of studies demonstrate linkages between above-ground and below-ground multitrophic interactions through plant defence strategies (Van der Putten *et al.* 2001; Bezemer *et al.* 2003; Bezemer & van Dam 2005; Soler *et al.* 2007; Kaplan *et al.* 2008a,b). Because of the different spatial and temporal scales at which the above-ground and below-ground multitrophic interactions operate, considering their individual and combined effects is supposed to enhance the understanding of how communities are structured and functioning. Most likely, this will also apply to facilitation.

Plant defences can be enhanced, or altered, by symbiotic interactions; for example, arbuscular mycorrhizal fungi in the roots may induce or enhance plant defence chemistry (Gange & West 1994), which influences above-ground trophic interactions (Bennett & Bever 2007). Plant defence can also be influenced by below-ground decomposers. Besides direct effects on below-ground plant enemies (Blouin *et al.* 2005), soil decomposers may have indirect effects on plant–above-ground enemy interactions through improving plant nutrition (Wurst *et al.* 2003, 2004; Bonkowski 2004; Bjornlund *et al.* 2006).

Considering a multitrophic perspective on plant–enemy interactions by including plant symbionts and plant–carnivore interactions will enhance our understanding of why some plant species can and others cannot be supported by a specific facilitator. Key to this understanding will be how plant relatedness influences sensitivity to second and higher trophic level interactions and to symbiotic mutualists. When plants benefit from plugging into mycorrhizal networks or from associations with symbiotic nitrogen-fixing microbes or endophytic mutualists, their relatedness should allow them to make use of these symbionts. The same applies to plants that attract ants, parasitoids or other carnivores for their defence against plant enemies. In all these multitrophic cases facilitation may be of dual benefit to those plants that have close relationships with their facilitators, as these relationships would enable them to benefit from these positive biotic interactions.

Relatedness between facilitators and facilitated plants may be less of an issue when considering decomposition and decomposer food webs, because decomposer organisms are supposed to have low specificity (Liiri *et al.* 2002). Nevertheless, in extremely low-resource environments, relatedness may play a role in resource acquisition, as some plant species use mycorrhizal fungi for short-cutting of nutrient cycles. For example, trees in Californian Pygmee forests have short-circuited the nitrogen cycle through nitrogen uptake by mycorrhizal fungi (Northup *et al.* 1995). Plant species that cannot make use of these mycorrhizal fungi may not be facilitated under such extremely low-resource conditions.

Interestingly, in a world-wide data base analysis, it was found that nurse species facilitated species that were more distantly related than expected based on a null model (Valiente-Banuet *et al.* 2006; Valiente-Banuet & Verdú 2007). In those studies, there was a clear relationship with fruit type, which suggested a relationship with seed dispersal, and the conclusion was that Quaternary plant species pull Tertiary plant species through time (Lortie 2007). In the same line of large-scale surveys, it was observed that facilitation among phylogenetically distant plant species turned into competitive relationships when phylogenetic distance decreased, probably because phylogenetically related species share the same niche (Valiente-Banuet & Verdú 2008). There is a need for more of those data base-mining studies and they need to be related to experimental studies. For example, there is a clear need for studies that analyse the 'biotic burdens and biotic benefits' that may go along with facilitation when considering that facilitated plants are plugging into the above-ground and below-ground multitrophic interactions of their facilitators.

Evolution of facilitation from a multitrophic perspective

Very little is known about how multitrophic interactions are involved in intra- and interspecific facilitation. Therefore, I will provide some, probably speculative, arguments to provoke thoughts for further research. To consider facilitation as a selective force, there should be variation that can be selected upon. Opposite to effects of variation in competitive responses, very little information exists on genetic variation in facilitative responses. Recently, Espeland & Rice (2007) demonstrated intraspecific variation for facilitation between populations of *Plantago erecta* in serpentine grasslands in California. The facilitation was supposed to be, at least in part, taking place below ground, but the precise mechanism remains to be resolved.

Intraspecific facilitation may be selected for when plants from the same species benefit from clustering, e.g. when enhanced densities of the same plant species may reduce the risk of predation (Hulme & Hunt 1999). The advantage of clusters of the same species could be that plants make use of the indirect defence systems, for example because of overlays with volatiles that are attractive to the parasitoids of herbivorous insects both above ground (Vos *et al.* 2001) and below ground (Rasmann *et al.* 2005). However, enhanced densities of the same plant species may also increase the incidence of attack by specialized pathogens (Burdon 1987; Carlsson *et al.* 1990; Carlsson & Elmqvist 1992; Ericson & Wennström 1997). This would favour frequency-dependent selection and it would probably select against intraspecific facilitation.

Interspecific facilitation can be detected by assessing the phylogenetic differences between facilitated plant species and their facilitators. For example, recently evolved plant species can preserve biodiversity over evolutionary time by facilitating anciently evolved plant species (Valiente-Banuet *et al.* 2006). In that case, anciently evolved plants may extend their historical time of occurrence even when climate has changed. On the other hand, the evolution of interspecific facilitation also can be considered as an extension of indirect defence of the facilitated plants. In that case, facilitated plants make use of the defences of their facilitators, which makes them trade-off indirect defence with another trait, e.g. germination and early growth under shaded conditions. Facilitation could also relax the need of plants to invest in direct defences, which may leave more energy to be invested in growth and competitiveness. Such strategies have been observed in invasive plants when released from natural enemies. Thinking along the same line, evolution may select for plant traits that enable sharing mutualistic symbionts with the facilitating nurse plants. In that case, facilitated plants could have been selected for using the mycorrhizal networks of their facilitators.

Finally, a question is whether there are selective forces against facilitation. Why would plants facilitate? Facilitation would evolve only if there is a benefit to it, or when the fitness of facilitators is not influenced negatively. There is some indirect evidence for this possibility coming from the biocontrol literature. When leek or carrots are undersown with white clover, they suffer from less thrips, rust fly and cavity spot infestation (Theunissen & Schelling 1998, 2000). If such interactions existed in nature, the benefit for the facilitator would be exposure to reduced insect or pathogen attack when facilitating. In that case, studies could determine whether there is a positive trade-off between resources taken away from the facilitator by competition with the facilitated plants and reduced enemy attack.

Mechanisms that may have negative effects on other plants, such as allelopathy, could be considered as a trait against interor intraspecific facilitation. Some studies have revealed that facilitated species can be adapted to the chemical compounds of their facilitator (Ehlers & Thompson 2004; Grondahl & Ehlers 2008). In that case, allelopathy could be considered as interference competition, as well as a mechanism selected for during facilitation: when individuals with the lowest allelopathic potential suffer the most fitness loss, selection will favour genotypes with the highest allelopathic potential. When the production of allelopathic compounds involves fitness loss, trade-offs may be searched for that weigh costs of allelopathic compound production against costs of fitness loss due to facilitation. This area clearly needs further experimental work to test how facilitating and facilitated plant species may evolve over time.

Conclusions and perspectives

Further understanding of the functioning and evolution of plant facilitation requires a multitrophic approach. Facilitating (nurse) plants are associated with a multitrophic above-ground and below-ground community of symbionts, herbivores, pathogens and their natural enemies. To be facilitated successfully, plants need to deal with the enemies of their facilitators, either by tolerance or resistance, or they should be able to make use of the predators and the mutualistic symbionts of their facilitators. Therefore, facilitation requires the ability to plug into the multitrophic network of the facilitators to avoid or resist enemies and to make use of symbionts and the enemies of the enemies (Fig. 2). Ultimately, the multitrophic network of the facilitator may be replaced by, or reshaped into, the multitrophic network of the facilitated plants.

Probably, the first selection sieve of the process leading to facilitation is formed by the abiotic conditions of the facilitating nurse plants, e.g. favourable germination sites. However, the filter immediately following abiotic conditions is the multitrophic community, as seedlings can be easily destroyed by spill-over pathogens and herbivores from the facilitator. The characteristics of the multitrophic community may be determined by the abiotic conditions, such as the degree of resource limitation or stress. Little is known about these abiotic effects on the structure and composition of the multitrophic networks. Intuitively, under low-resource and high-stress conditions symbiotic relationships may provide the strongest biotic sieve. However, the current literature also includes examples where natural enemies play an important role in such extreme conditions. Clearly, more studies are required to determine general patterns of how above-ground and below-ground multitrophic interactions develop along resource and stress gradients and how this influences facilitation.

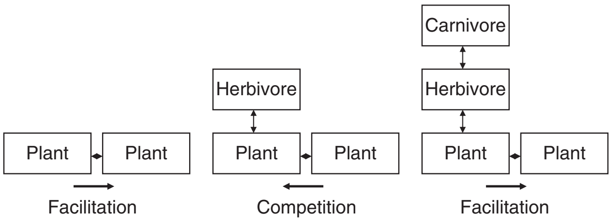

Fig. 2. Basic scheme of how adding the second trophic level (a specialist herbivore of the facilitator) may turn facilitation into competition and how addition of the enemy of the herbivore makes that competition turn back into indirect facilitation. All other mechanisms used in the text can be visualized by changing the interactions and the complexity of this basic scheme.

Considering biotic interactions between plants, symbionts, herbivores, pathogens and their enemies reveals that the difference between competition and facilitation becomes even more transient than proposed before by Callaway & Walker (1997) and Holmgren, Scheffer & Huston (1997). Symbionts and decomposer organisms may enhance the competitive strength of their hosts, whereas herbivores and pathogens may weaken their hosts' competitive ability. The role of plant symbionts and plant enemies depends on their focal activity: symbionts that enhance the performance of rare species, and herbivores and pathogens that reduce the performance of dominant plant species all may facilitate species replacement and enhance plant community diversity (see fig. 3 in Wardle *et al.* (2004)). On the other hand, when symbionts enhance the performance of dominant plants, and herbivores and pathogens reduce that of rare plants, they increase competition and weaken facilitation. Therefore, plant–enemy and plant–symbiont interactions may turn facilitation into competition and competition into facilitation, depending on the focus and mode of interaction with symbionts and plant enemies. When extending this perspective to higher trophic level interactions, cascade-like effects may occur (Fig. 2).

In conclusion, research on plant facilitation requires a more explicit consideration of interactions between plants, symbionts, herbivores, pathogens and their enemies, as these co-determine the functioning and evolution of plant–plant interactions. Plant facilitation requires that the facilitated individuals are successful in plugging into the above-ground and below-ground multitrophic interaction web of their facilitators. Therefore, these multitrophic interactions have a potential for selection and the evolution of facilitation, when genetic variation for these effects exists in facilitating and facilitated populations.

This plugging into the facilitators' multitrophic interactions can probably contribute to explaining patterns in phylogenetic similarity or dissimilarity between the facilitators and the facilitated species. Clearly, a major part of these biotic interactions take place below ground and ultimately, research on plant facilitation requires an explicit above-ground–below-ground multitrophic perspective to enhance our capacity of understanding and predicting plant–plant interactions now and in response to global changes in land use, climate and atmospheric composition.

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