Trends in
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Review

Facilitation and plant phenotypic evolution

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While antagonistic interactions between plants have been a major topic of eco-evolutionary research, little evidence exists on the evolution of positive plant interactions (i.e., plant facilitation). Here, we first summarize the existing empirical evidence on the role of facilitation as a selection pressure on plants. Then, we develop a theoretical eco-evolutionary framework based on fitness-trait functions and interaction effectiveness that provides predictions for how facilitation-related traits may evolve. As evolution may act at levels beyond the individual (such as groups or species), we discuss the subject of the units of evolutionary selection through facilitation. Finally, we use the proposed formal evolutionary framework for facilitation to identify areas of future research based on the knowledge gaps detected.

Highlights

Plant facilitation is a crucial interaction shaping past and present communities, but its evolutionary potential as a selective force is currently unknown.

An evolutionary framework based on fitness-trait functions and the effectiveness of the interaction provides clear predictions about the evolution of facilitation traits.

The evolutionary potential of facilitation may go beyond the individual and act at different levels (groups and species).

Facilitation as a selection pressure on plants

Plant **facilitation** (see Glossary) shapes ecological communities [1] acting as an important driver of biodiversity [2]. Facilitation can occur between a wide range of organisms, but is particularly well-explored among plants (i.e., **benefactors**) that allow the establishment and enhance the fitness of other plants (i.e., beneficiaries) [3]. Plant facilitation, although most evident in harsh environments, is widespread in nature, ranging from polar [4,5] and alpine [6,7] ecosystems, over desert [8,9] and semiarid [10] environments, to grasslands [11], crop fields [12,13], savannahs [14], and forests [12,15].

The ubiquity of facilitation, together with the sessile nature of plants that causes long-term stable associations, makes plant facilitation particularly suitable to act as a selective force. Indeed, facilitation is expected to have evolutionary consequences for the **beneficiary** [16–19] and the benefactor species [2,20–22], as empirically demonstrated in a few studies [23,24]. Such a limited number of studies is surprising given that facilitation has been considered, at least theoretically, to be a selective force [3,18,25–29].

Here we synthesize empirical evidence on the role of facilitation as a selection pressure on beneficiary plants. We argue that the lack of a formal evolutionary framework with clear premises and predictions has hindered research on the evolution of facilitation. After reviewing experimental studies suggesting that facilitative behavior evolves, we propose an evolutionary framework based on fitness–trait functions and interaction effectiveness, and provide an example that could serve as a guide for future studies on the evolution of facilitation. Finally, we discuss the levels of selection beyond the individual at which facilitation appears to act. We also highlight crucial knowledge gaps and raise outstanding questions aimed to foster future research.

Evidence of the evolutionary impact of facilitation

It has been widely shown that ecological interactions may evolve themselves. For instance, mutualistic interactions seem to have evolved multiple times from commensalistic and antagonistic interactions [25]. Similarly, facilitative interactions may also evolve from non-facilitative ones and vice versa.

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Crop domestication is a long-running process showing that facilitation may indeed evolve in plants. Human-driven selection of individuals with beneficial traits for food production has a history of over 10 000 years [30]. While some domestication processes have favored species with facilitative traits to be grown in polycultures, industrialized farming and breeding have favored species with competitive traits to be grown in monocultures under high external inputs. Both cases provide evidence that facilitation traits may evolve [31]. Among the domestication processes using facilitation and niche differentiation is the so-called 'milpa', a maize-based highly integrated system of food production along with squash and beans, in which pre-Columbian inhabitants promoted the adaptation of plants to both physical and biotic environmental conditions. Its cultivation consists of selecting seeds that are grown with neighbors of other species [32] and yield higher total production than when growing in monoculture [33–35]. This overyielding has been explained as a result of enhanced niche differentiation and facilitation ([34,35] and references therein). Species complementarity is displayed in the differences among species in root architecture leading to different rates of nutrient uptake, shoot architecture triggering differential growth, and interactions with nitrogen-fixing bacteria promoting nutrient transfer among species [35–37].

By contrast, industrialized varieties have been bred for uniformity and show reduced trait variability, and therefore a reduced potential for complementarity effects [38]. Indeed, recent research has compared complementarity effects among crops with that of their wild relatives and found that complementarity was significantly reduced among crops [39]. In line with this, grassland species with a history in monocultures also showed reduced complementarity effects compared to those with a history in mixture [31]. Increased complementarity in this study was demonstrated through increased character displacement [i.e., increased differences in plant height and specific leaf area (SLA), and increased functional diversity overall] in plant communities with a mixture history. The reduced complementarity effects of species with monoculture origin could indeed be attributed to less frequent and less intense facilitative interactions [40], providing to date the only direct evidence that plant facilitation can evolve and be lost depending on the biotic environment. Based on the same study system, van Moorsel et al. [41,42] also showed that rapid evolution over only 12 years selected for monoculture and mixture types of plant species, each with a distinct facilitation potential [40].

The evolution of facilitation should entail the evolution of traits of the beneficiary plants. Benefactors facilitate their associated plants through the construction of favorable niche space by accumulating nutrients, providing shade, or protecting from herbivores [6]. This niche construction may impact selection in the wild [43]. A recent meta-analysis on selection gradients of animal traits evolving under organism-constructed and unconstructed microhabitats revealed differences in the magnitude and variance of natural selection [44]. It is tempting to conjecture from these results that, in the context of facilitation, benefactor species will construct niche space for other species and act as selective agents for the evolution of traits of beneficiary species.

Traits of beneficiary plant species tend to differ from those of their benefactors and strongly depend on the community where facilitation occurs. For example, in American deserts beneficiaries are large-seeded, tall species that greatly invest in roots [45]; in Mediterranean-type ecosystems they are animal-dispersed, evergreen, long-rooted, resprouter species with large leaves [46]; and in stressful abandoned mine tailings in Eastern Spain they are short, non-resprouter species with small leaves and short roots [47,48]. The final outcome of the facilitation interactions will depend not only on the traits of the beneficiaries but on the interaction of these traits with those of the benefactors [49,50]. In more general terms, in contrast to generally stress-tolerant benefactors, beneficiaries tend to have traits that increase their competitive ability [51,52], most likely due to the

Glossary

Benefactor: the plant that produces a positive effect on the beneficiary plant. Sometimes called nurse or facilitator.

Beneficiary: the plant expressing a positive response to the presence of a benefactor plant. Sometimes named facilitated plant or facilitatee.

Facilitation: the positive effect of a neighboring plant on the fitness of a target plant without negative consequences for the neighbor.

Facilitation effectiveness (FE): the number of beneficiary plants established as a consequence of the interaction with the benefactor.

Quantity component of effectiveness (QTC): the number of seeds of the beneficiary species arriving underneath a given benefactor.

Quality component of effectiveness (QLC): the probability of seeds arriving underneath a benefactor to reach adulthood and reproduce successfully due to the multiple positive effects of that benefactor.

fact that beneficiaries benefit from stress amelioration by the benefactor and compete with the rest of beneficiaries for the available resources [53]. Indeed, latest research showed that populations adapted to growth with a benefactor had increased competitive ability compared to populations of the same species adapted to grow in isolation [24]. Altogether, these studies suggest that facilitation may mediate trait evolution.

An evolutionary framework for facilitation-mediated phenotypic evolution

For facilitation to mediate phenotypic evolution, two processes should occur: (i) the fitness of the individuals associated with neighbors should be greater than that of isolated individuals; and (ii) this benefit on fitness should be caused by the presence of a given trait in the target species. Many studies have addressed the net effect of neighbors on the fitness of target plants, mostly by comparing fitness with and without a neighbor (Figure 1A–C). Only when the neighbor behaves as a benefactor increasing the fitness of the target plant is the interaction considered facilitation (Figure 1A). Indeed, much is known about the outcome of facilitation for the target species as a function of the ecological and phylogenetic characteristics of their neighborhoods [29,54]. However, to understand how plant–plant interactions can shape beneficiary plant phenotypic evolution, it is critical to determine the interaction-mediated relationship between the fitness and the phenotype of the beneficiary individuals (Figure 1D–F). This question has barely been addressed empirically because most of these studies have estimated the effects of benefactors on the fitness of the beneficiaries without considering the trait(s) mediating the interaction, an
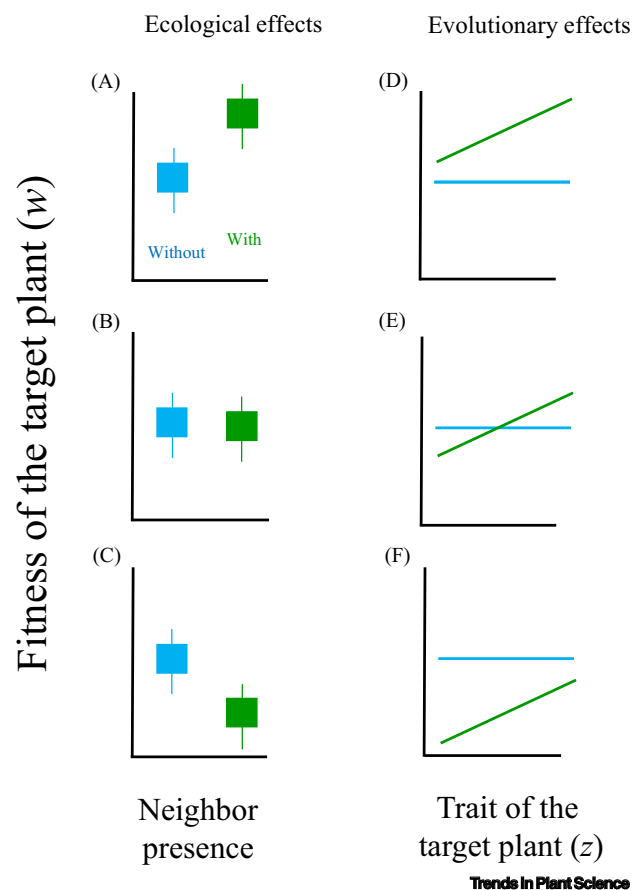

Figure 1. Ecological and evolutionary effects of neighbors. Neighbors may affect the fitness (w) of the target plant positively (A), neutrally (B), or negatively (C). Different evolutionary effects may emerge when a given trait is related to the fitness of the plant in each of the three scenarios: positive (D), neutral (E), and negative (F). Facilitation and facilitation-mediated evolution only occurs in the positive scenario (A and D, respectively). For facilitation to have evolutionary effects, the neighbor should affect the relationship between fitness (w) and the trait (z) of the target plant (fitness–trait function). In this example, we illustrate a simple situation in which the trait affects the fitness of the target plant positively when growing with a neighbor (green lines) but does not affect fitness when growing in isolation (slopes of the trait–fitness relationship equal to zero, blue lines) (D). Note that fitness–trait functions may have different slopes and be even nonlinear. The only condition is this fitness–trait function would be significantly different in presence and absence of neighbors. Note also that this difference in fitness-trait function may also happen when the neighbor has neutral (E) or negative (F) ecological effects. Summing up, for facilitation to mediate selection on traits, the neighbor must not only enhance the fitness (A) but also modify the relationship between fitness and phenotype of the target plant (D).

approach that lacks crucial information from an evolutionary point of view [55]. Evidence for facilitation exerting selective pressure on beneficiary plants requires demonstrating that the relationship between the phenotypic trait and the fitness of the beneficiary plant is modified in the presence of the benefactor species (Figure 1D). In other words, the occurrence of facilitation-mediated selection on a given trait requires the existence of a significant interaction between the trait value and the presence of the benefactor.

A successfully framework to study ecological interactions is the so-called interaction effectiveness [56,57]. Under this framework, the effect of a given interacting organism on the fitness of its partner depends on the multiplicative effects of two components: (i) the quantitative component of effectiveness (QTC); and (ii) the qualitative component of effectiveness (QLC). The QTC measures the number of immediate interaction outcomes whereas the QLC incorporates the post-interaction, delayed outcomes of the interaction [56]. For example, pollination effectiveness is usually defined as the number of viable seeds produced by the interaction between a pollinator and a plant, whereas QTC is defined as the number of pollen grains deposited by the pollinator and QLC is the probability of a pollen grain producing a viable seed [56]. In the context of facilitative interactions, facilitation effectiveness can be defined as the number of beneficiary plants established as a consequence of the interaction with the benefactor; QTC can be defined as the number of seeds of the beneficiary species arriving underneath a given benefactor; and QLC can be defined as the probability of these seeds to reach adulthood and reproduce successfully due to the multiple positive effects of the benefactor (microhabitat amelioration, herbivore protection, nutrient sharing, etc.). The effectiveness of a given benefactor depends on the beneficial effects provided through QTC, QLC, or both components (see Figure IA in Box 1).

The effectiveness framework can be used to explore how benefactors may drive the evolution of beneficiary traits. Benefactors may select for traits of the beneficiary by increasing the probability of interaction (named 'attraction trait' in animal–plant interactions), and/or the fitness of the beneficiary once the interaction has occurred (called 'matching traits' in animal–plant interactions). In Figure IB in Box 1, we illustrate this idea using a well-studied system, the facilitation of holm oaks (*Quercus ilex*) by several benefactors. Overall, our effectiveness analysis suggests that facilitation will mediate the evolution of large acorns, through both the quantity component, larger acorns arriving at superior benefactors, and through the quality components, large acorns recruiting better than small acorns under these benefactors (see Figure IB in Box 1).

In order to foresee how facilitation may favor the phenotypic evolution of beneficiary plants, we have modelled the consequences of selection through QTC and QLC (Figure 2). These models

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Box 1. Interaction Effectiveness framework applied to facilitation

Benefactor plants may differ in **facilitation effectiveness (FE)** as a consequence of their variation in quantitative component of effectiveness (QTC) and qualitative component of effectiveness (QLC). An intuitive way of illustrating this variation is through the effectiveness landscape, a two-dimensional space where all combinations of QTC and QLC yielding the same FE values are connected by isolines [56]. For example, in the hypothetical situation depicted in Figure IA, the FE of the benefactor represented as a black dot is high due to the combination of high QLC and QTC values, whereas the FE of the other benefactors is lower because either one or both components have low values. This approach can be applied to real-world systems. Using the information from many sources [87–102], we have inferred the FE of Holm oaks (*Quercus ilex*) facilitated in the Iberian Peninsula by three types of benefactors, pines, shrubs, and conspecifics (Figure IB). In this system, the effect of each benefactor is partially influenced by the size of the oak seeds. Big seeds, transported mostly by corvids, arrive mostly under pines. The probability of these seeds of surviving to sapling (a proxy of the QLC) is highest when located under pines. As a consequence, the FE of pines as a benefactor of big seeds is much higher than that of shrubs and conspecifics. By contrast, small seeds, transported mainly by rodents, arrive mostly under shrubs, although the QLC of this benefactor is very low and almost no small seed can recruit under them. Pines are also poor benefactors of small seeds, due to their low values of QTC. According to this effectiveness landscape, we would expect an evolution toward larger acorns in oaks growing in pine-oak forests.
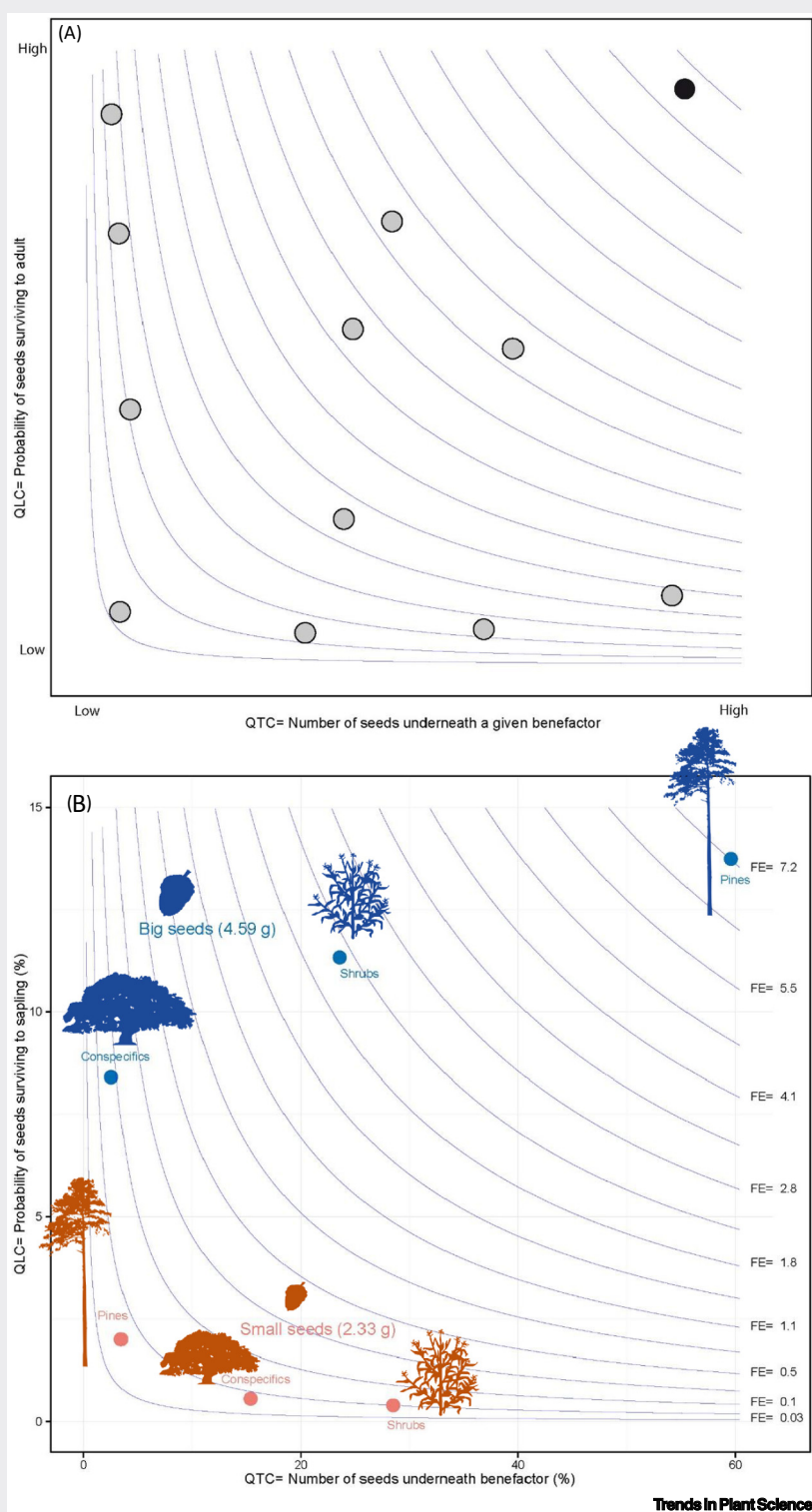
Figure I. Hypothetical (A) and real (B) effectiveness landscapes of facilitation interactions.
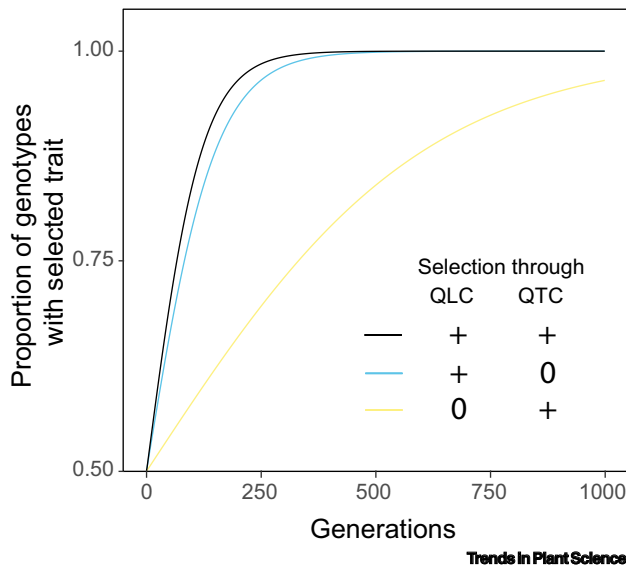
Figure 2. Facilitation-mediated trait evolution in beneficiary plants. This graph describes the number of generations necessary for the fixation of a binary trait state when it is favored by facilitation as a consequence of the selection acting through the quantity (QTC) and/or quality (QLC) components of the facilitation effectiveness. A trait state is fixed when the proportion of the genotypes bearing that state is 1.0. In all cases, the selection differential acting on the trait state was s = 0.02 and was calculated following Endler [86] as 1.0 - (Fitness of the individuals with non-selected trait/Fitness of individuals with the selected trait). We considered the selected trait as that having highest fitness. The skeleton model is based on a stage structured population model. It assumes that all traits have equal evolvability. The initial frequency of the two trait states was 0.5. Abbreviations: QLC, qualitative component of effectiveness; QTC, quantitative component of effectiveness.

show that the rate at which a given trait is fixed in the population is faster when facilitation-mediated selection acts through both components in the same direction (black line, Figure 2) or through QLC alone (blue line) than when it acts through QTC (yellow line, Figure 2). That is, our model suggests that those plant traits that increase the probability of establishment under a benefactor will be selected more easily than those traits that increase the probability of interaction. This outcome may explain why little empirical evidence exists on the evolution of traits affecting the probability of facilitation to occur, despite the profusion of studies focusing on microhabitat-dependent recruitment. For example, it has been suggested that the production of pilosus achenes by wind-dispersed Asteraceae helps seeds to get trapped by benefactor shrubs in some arid ecosystems [58]. Similarly, fruit traits favoring the interaction with frugivores using perches versus latrines [59] could be selected not only by seed dispersal but also by facilitation. Further research on the evolution of traits allowing seeds to move toward benefactors is necessary to get a full understanding of how facilitation may select for traits through QTC.

The QLC of the interaction is still poorly understood despite the increasing availability of trait-based facilitation studies [60,61]. Most of these studies have been performed at the interspecific level, finding that species that benefit more from facilitation have different traits (usually related to a resource-acquisitive strategy) than those not requiring facilitation [62]. Trait differences have been also found at the intraspecific level. For example, *Helleborus foetidus* individuals growing associated to benefactor shrubs show larger SLA, lower water use efficiency, and higher fitness than individuals living alone [63]. However, these type of studies cannot explain how traits evolve. To unambiguously demonstrate trait selection through QLC, the fitness of the beneficiary plants associated to benefactors should be dependent on their trait values, as per Figure 1D. By using genetically-modified *Arabidopsis thaliana* individuals with low tolerance to salt, Zhang and Tielbörger [64] found that under high salinity conditions, plants survived and reproduced more when growing with neighbors, and such a benefit was larger for salt-sensitive than for salt-tolerant individuals. That is, these authors show a relationship between a trait (salt tolerance) and individual fitness when growing with benefactors. This finding suggests that facilitation can select for particular traits of beneficiary plants through QLC.

Units of selection in facilitation

Theories explaining the evolution of new biological structures, like endosymbiosis, kin selection, and group selection, have invoked positive interactions. That is why Kikvidze and Callaway [65] argued 'that facilitation between individuals at different levels of biological organization can act as a cohesive force that generates a new level of organization with higher complexity and thus allows for major evolutionary transitions at all levels of biological hierarchy'. Up to this point, the cases we have reviewed linking facilitation to evolution can be understood considering natural selection acting at the individual level. In this section, we discuss other examples in which facilitation has been proposed to act at different organizational levels and the traits that could be involved in the interaction.

Kin selection

Kin selection refers to the evolution of behaviors favoring the fitness of relatives. Although plant facilitation has mainly focused on interspecific interactions, intraspecific facilitation in general, and between relatives in particular, has been known for some time [66]. Intraspecific facilitation is strongly mediated by the presence of mycorrhizae [67,68]. Kin selection is one of the scenarios that could explain this pattern because common mycorrhizal networks connect plants, facilitate nutrient and defense transfer, and allow kin recognition [69]. For example, Pickles *et al.* [70] have shown that carbon transfer through mycorrhizal networks is much higher between full-sibs than between unrelated seedlings.

Further evidence comes from studies demonstrating kin recognition in plants and its positive effects on plant fitness. For example, individuals of *Moricandia moricandioides* surrounded by kin produced larger flowers and attracted more pollinators than individuals surrounded by non-kin [71]. Higher pollinator attractiveness was to the benefit of the whole patch of related individuals, therefore resulting in mutualistic facilitation. Other studies have identified that root exudates mediate kin recognition in plants [72]. However, the steps necessary to demonstrate unambiguous support for kin selection are very challenging [73], resulting in limited evidence that intraspecific beneficial interactions between kin goes along with kin selection.

Group selection

Group selection refers to selection operating not between individuals but between groups of individuals, resulting in the evolution of group-advantageous traits. For facilitation to select a trait through this process, the trait (z) of the group would have to increase the fitness of the group (w) only in the presence of a benefactor (as in Figure 1D). The trait of a group is not a property of the individuals but an emergent property of the collective group. For example, a diverse floral display due to the synchronic flowering of a group of individuals can be considered a trait of the group rather than a trait of each individual plant. Similarly, the fitness of the group refers to the differential reproduction of a group relative to other groups.

Although highly debated, group selection has been invoked to explain intraspecific facilitation at the seedling and adult stages of the southern beech tree, *Nothofagus pumilio* [74,75]. Under stressful environmental conditions, tree seedlings showed higher survival rates at increasing densities of conspecifics [74], while adult trees showed higher survival rates when merged with conspecific individuals compared to unmerged individuals [75]. Thus, the authors argue that facilitation promotes adult merging, a group-level trait under selection. The extent to which merging is a group-level trait directly related to the fitness of the group is still unclear. Group selection in plants has been demonstrated [76] and therefore, the possibility that facilitation could be behind deserves further research.

Species selection

Species selection refers to differences in net diversification rates associated with particular heritable traits and their environmental interactions [77]. A recent review has shown that traits that increase fitness in a positive interaction might increase diversification rates by buffering species from extinction and/or increasing speciation rates through divergent selection and reproductive isolation [78]. However, facilitation can interfere with speciation events. Theory suggests that facilitation can impede speciation through enabling gene flow between differently adapted populations in a habitat [79]. This seems to be the case of *Euphorbia nicaeensis* facilitated by the dominant shrub *Juniperus sabina* [80]. Even though *Euphorbia* populations beneath the shrubs and on the open ground showed flowering phenology differences, there was no indication for genetic differentiation among the populations. This is in line with other research showing that a phenological mismatch of a species between different microhabitats does not necessarily result in genotypic differentiation [81].

In the opposite direction, theoretical models also predict that facilitation may promote speciation through the colonization of and local adaptation to otherwise unsuitable habitats [79]. This theoretical expectation opens the possibility of facilitation to be a force of species selection. If this is true, then a species-level trait (z) should increase the 'fitness' (w) of that species, that is, the number of their descent species or, in other words, the diversification rate of its lineage. For example, plant traits involved in insect pollination increase diversification rates by promoting pollinator specificity and reproductive isolation among plant species [82]. In the context of facilitation, a recent study suggested that both competitive and facilitative plant interactions can drive plant diversification [83]. These authors characterized plant–plant associations through the relative interaction index RII, a metric explaining whether plants were positively (i.e., facilitation), negatively (i.e., competition), or nonassociated to neighbors, and showed that RII was conserved within genera and associated to the number of species per genus. These results suggest that traits underlying the frequency of plant–plant associations might be considered as heritable traits associated to diversification, the required premises for species selection. Linking particular plant traits to RII to formally test whether facilitation promotes species selection in a macroevolutionary context deserves future research.

Concluding remarks and future perspectives

Benefactors are constructors of niche space, and this in turn may modulate not only the survival of other species but also the evolution of their traits. We propose here a research program aimed at demonstrating the evolutionary importance of facilitation. First, this research program might be trait-based, meaning that the traits involved in the interaction should be explicitly considered. As a consequence, the relevant unit of observation should be the individual. Furthermore, this research program should explore the association between these traits and the fitness of the plants, a prerequisite for selection to occur. It is widely known that for natural selection to produce adaptations, traits have to be heritable. Although significant heritability is known for competitive ability traits [84,85], little is known for facilitation traits. Consequently, heritability of facilitation traits should also be determined within the context of our evolutionary research program. Finally, we also think that future studies on facilitation might benefit from considering the effectiveness framework, that differentiates those traits that increase the occurrence of interaction from those enhancing the outcome of the interaction. The integration of this information in a common trait-based effectiveness framework considering other plant interactions (pollination, seed dispersal, mycorrhiza, etc.) could shed light on the relative importance of facilitation as an evolutionary motor of plants (see Outstanding questions).

Outstanding questions

Can facilitation act as a selective force?

Does selection favor traits that increase the probability of facilitation?

Has plant domestication modified facilitation traits?

Can facilitation promote evolutionary diversification?

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Declaration of interests

There are no interests to declare.

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