

EDITORIAL

Facilitation in communities: underlying mechanisms, community and ecosystem implications

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Introduction

Facilitation (positive interactions among organisms) in communities has been the subject of increasing interest for community ecologists since the mid-nineties (Fig. 1), although this is a pioneer core concept in community theory, proposed a 100 years before this issue by Clements (1916), as the main driving biotic mechanism of plant community succession. However, it was neglected by most community ecologists for decades due to the overwhelming popularity at that time of the individualistic (Gleason 1926; Whittaker 1956) and competition theories (Grime 1974; Tilman 1982). Until the mid-nineties, competition was by far the most studied biotic interaction, in particular by plant community ecologists (see Fig. 1: more than 90% of the biotic interactions studies published at that time concerned only competition). However, due to the increasing evidence of facilitation in experiments conducted in severe conditions from marine intertidal and terrestrial environments, Bertness & Callaway (1994) proposed a conceptual model where competition switches to facilitation with increasing environmental severity. Since then, and during the following two decades, the interest in facilitation has never ceased to increase (see Fig. 1: currently only 76% of the biotic interactions studies concerns only competition).

During the first half of this period of emergence of facilitation as an important research area, a number of conceptual studies evidenced the multiple community and ecosystem implications of facilitation (Callaway 1995, 1997, 1998; Pugnaire, Haase & Puigdefábregas 1996; Callaway & Walker 1997; Hacker & Gaines 1997; Holmgren, Scheffer & Huston 1997; Brooker & Callaghan 1998; Stachowicz 2001; Bruno, Stachowicz & Bertness 2003; Lortie *et al.* 2004; Armas & Pugnaire 2005; Brooker 2006; Padilla & Pugnaire 2006), and many empirical studies focused on the experimental test of the pioneer model of Bertness & Callaway (1994) (e.g. Pugnaire & Luque 2001; Callaway *et al.* 2002; but see Callaway 2007 and Brooker *et al.* 2008 for reviews). Facilitation became

during this period a well-established phenomenon. However, a strong controversy questioned in 2005 the importance of facilitation in dry environments and, thus, the validity of the Stress Gradient Hypothesis (Maestre, Valadares & Reynolds 2005; Michalet 2006, 2007; Maestre *et al.* 2009; but see Lortie & Callaway 2006; Armas, Rodríguez-Echeverría & Pugnaire 2011). This controversy was followed by the publication of other alternative models to the SGH, proposing a collapse of facilitation in extremely stressful conditions (Michalet *et al.* 2006, 2014a; Xiao *et al.* 2009; Holmgren & Scheffer 2010; Verwijmeren *et al.* 2013; Le Bagousse-Pinguet *et al.* 2014a). At this time of important conceptual refinement, a European Science Foundation meeting was held in Arcachon (France) in 2006, the conclusions of which were collected in a highly cited publication (Brooker *et al.* 2008; see Fig. 1). Brooker *et al.* (2008) also highlighted several key issues for developing future facilitation studies which were the main basis of a BES symposium organized in 2009 in Aberdeen and the subsequent special issue in the *Journal of Ecology* (Brooker & Callaway 2009; see Fig. 1). The main goal of the BES symposium and special issue was to open facilitation research to new directions, and to actively develop conceptual links with other research fields from which research on facilitation would profit, such as evolutionary ecology, restoration ecology and marine sciences.

Since then, the field has moved incredibly fast (Fig. 1). There have been many important and novel recent advances, such as the assessment of the evolutionary consequences of facilitation (e.g. Michalet *et al.* 2011; Thorpe *et al.* 2011; Butterfield *et al.* 2013), the feedback effects between facilitator and facilitated species (e.g. Schöb *et al.* 2014a,b,c), the functional consequences of facilitation (e.g. Schöb, Butterfield & Pugnaire 2012; Butterfield & Callaway 2013; Schöb *et al.* 2013) or the interactions with below-ground organisms (e.g. Hortal *et al.* 2013; Rodríguez-Echeverría *et al.* 2013). Several meta-analyses and theoretical studies have further analysed the relevance of the SGH with contrasting results or conclusions (He, Bertness & Altieri 2013; He & Bertness 2014; Michalet *et al.* 2014a,b; Soliveres & Maestre 2014; Soliveres, Smit & Maestre 2015; and see Armas, Rodríguez-Echeverría & Pugnaire 2011; Pugnaire *et al.* 2015). However, as

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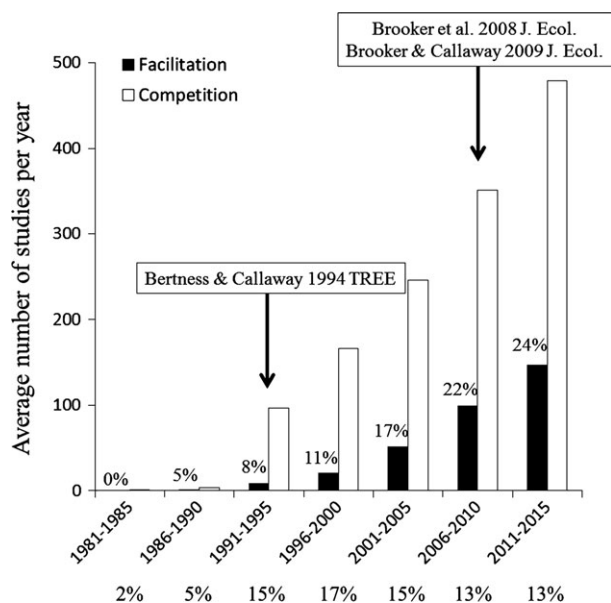


Fig. 1. Average number of studies per year for facilitation (black bars) and competition (white bars) in the plant community literature every 5 years since 1981. Numbers above black bars are the percentages of facilitation studies relatively to all biotic interactions studies (facilitation and competition) in the plant community literature, whereas numbers below horizontal labels are the percentages of biotic interactions studies (facilitation and competition) relatively to the plant community literature. The two arrows above bars indicate the dates of publication of the pioneer model of facilitation (Bertness & Callaway 1994) and of the report papers on two important facilitation meetings (Brooker *et al.* 2008, for the ESF Arcachon (France) meeting in 2006, and Brooker & Callaway 2009, for the BES Aberdeen (UK) meeting in 2008).

Pakeman *et al.* (2009) asked after the Aberdeen symposium, we believe that the field of facilitation will soon reach a kind of maturity, beyond conceptual confrontations and the simple picture of greater facilitation in stressful environments (Semchenko 2016). As in the Grime-Tilman competition debate of the eighties and early nineties, most community ecologists are now aware that no single theoretical model may explain the occurrence or disappearance of facilitation along environmental gradients. Nature is by far much more complex than our simple conceptual models, and we rather keep deepening our knowledge on the mechanisms of facilitation and their community and ecosystem implications.

The main goal of this Special Feature is to go back to the basics of facilitation, trying in particular to review knowledge on the main functional mechanisms of facilitation (papers 1–4), their implications for community structure (papers 5–8) and ecosystem functions and services (papers 9 and 10). This Special Feature complements the Special Feature on mechanisms of competition published in the journal in 2013 (Robinson, Trinder & Brooker 2013). The authors represent a large panel of specialists in positive interactions in ecological communities, and extend far beyond the main core group of facilitation researchers. The preparation of this Issue was closely aligned with a

meeting held in Baeza (Spain) in September 2014, and we acknowledge all participants of the meeting for their helpful comments which certainly improved the quality of this Special Feature.

Underlying mechanisms of facilitation

Butterfield *et al.* (2016) address one of the most contentious debates surrounding the stress gradient hypothesis (SGH), the relationship between water limitation and facilitation. As mentioned above, this topic was hotly debated after 2005. Butterfield *et al.* (2016) take here a close look at the role of soil moisture in mediating plant–plant interactions. By assessing the effects of climate and soil texture on this process and using an empirically parameterized soil moisture model, Butterfield *et al.* (2016) simulated soil moisture dynamics beneath shrubs and gaps using data from 1000 sites in the Western United States. They found that difference between soil moisture under shrubs and in gaps decreased along the aridity gradient when long-term average conditions were considered, contrary to expectations based on the SGH. However, when extreme years were considered, positive effects of shrub on soil moisture were greatest at intermediate points along the spatial aridity gradient, consistent with a hump-backed model of plant–plant interactions (Michalet *et al.* 2006; Holmgren & Scheffer 2010). These results suggest that plant effects on soil moisture are predictable, and highlight the importance of accounting for temporal and spatial heterogeneity in determining plant–soil moisture relationships. Rather than focusing on SGH predictions, it may be more beneficial to explicitly incorporate plant effects on soil moisture into predictive models of plant–plant interaction outcome in drylands.

In a related paper, Metz & Tielbörger (2016) address the role of plant–plant interactions in modifying the impact of climate change on plant communities. The magnitude and even direction of plant interactions in response to environmental changes – based on spatial gradients – remains highly debated, especially in water limited ecosystems. Unfortunately, mechanistic experimental manipulations are rare compared to correlative approaches that infer patterns from observations along spatial climatic gradients, and predictions using these approaches range from increasing facilitation to increasing competition with future aridification. Metz & Tielbörger (2016) argue that the methodology used for assessing plant–plant interactions may greatly affect the outcome. In this paper, Metz & Tielbörger (2016) use a unique climatic gradient combined with large-scale, long-term manipulations to test whether predictions about plant–plant interactions yield similar results when using experimental manipulations, spatial gradients or temporal variation. They assessed shrub–annual plant interactions in three different sites along 27 natural rainfall gradients (spatial) during 9 years of varying rainfall (temporal) and 8 years of dry and wet manipulations of ambient rainfall (experimental) that closely mimicked

regional climate scenarios. The results differed greatly among approaches. Experimental water manipulations hardly altered shrub effects on annual plant communities. Along the spatial gradient, shrub effects shifted from clearly negative to mildly facilitative towards drier sites, whereas temporal variations showed the opposite trend: more negative shrub effects in drier years. Based on their combined approach, Metz & Tielbörger (2016) conclude that shrub-annual interactions will remain unaltered under future climates. This conclusion contrasts with the suggestion made by space-for-time studies based on spatial gradients that facilitation should increase with climate change. Long-term experimental manipulations appear to be critical for evaluating climate change impacts. Metz & Tielbörger (2016) also showed that correlative approaches may be misleading, overestimating the response of plant-plant interactions to climate change.

Despite growing evidence that soil microbiota impact plant fitness and community dynamics, their role in plant facilitation has been little explored to date. Rodríguez-Echeverría, Lozano & Bardgett (2016) synthesize in this Issue the scant evidence available on the effect of nurse plants on abundance, composition and activity of soil microbial communities, addressing feedback effects between nurses and beneficiary plant species. Evidence suggests that nurses promote larger, differentiated soil microbial communities with high activity, and the dominance of competitive bacteria and larger mycorrhizal networks, as compared to adjacent soils without nurses. Such microbial communities have positive effects on the establishment, growth and fitness of beneficiary plant species through a variety of mechanisms, including increased nutrient availability, soil stabilization and niche complementarity, but also direct molecular signalling between soil microbes and plants that affect plant defence and interactions. Although evidence on the role of soil microbes on nurse plant facilitation is mounting, there are still only a few studies from which to draw general conclusions. The field is still in its infancy, and further research is needed to understand the precise role of soil microbes and the mechanisms they use to influence facilitation between plants.

Facilitation studies to date have focused primarily on plants, often neglecting the extended effects that cascade through ecological networks. Lortie, Filazolla & Sotomayor (2016) propose in this Issue a conceptual framework that explores positive interactions including the functional roles of the interacting species, and to quantitatively summarize the current state of this field examining effects beyond plant-plant interactions. A limited number of studies have examined the importance for animals of benefactor-subordinate plants association. Selecting 36 studies which documented positive plant interactions, Lortie, Filazolla & Sotomayor (2016) generated a total of 53 independent instances of either shrub-plant-animal or shrub-animal-plant interactions. These interactions were split between direct and indirect interactions between shrubs and animals. Hypotheses frequently tested included

effects of seed trapping, herbivore protection, magnet pollination and facilitation-mediated secondary seed dispersal. The most common functional role of shrubs was protection from herbivory, and the most common animal role associated with plant-facilitation complexes was that of a consumer. Lortie, Filazolla & Sotomayor (2016) conclude that multitrophic, integrated sets of experiments incorporating plant facilitation into models of community dynamics are critical in advancing management of high-stress ecosystems wherein positive interactions are commonly reported.

Community implications

A set of papers focuses on the implications of facilitation for community diversity and the feedback effects for the nurse species, in ecosystems ranging from alpine to arctic to marine and terrestrial in general. The role of facilitation in community diversity is one of the best known implications of facilitation (Hacker & Gaines 1997; Pugnaire & Lázaro 2000; Bruno, Stachowicz & Bertness 2003; Michalet *et al.* 2006; Cavieres & Badano 2009). However, this effect has been primarily studied at the patch level, that is comparing diversity of associated plants within nurse patches vs. away from them in adjacent open areas, in particular in alpine communities (e.g. Cavieres *et al.* 2014). In this Issue, Cavieres *et al.* (2016) review the literature in alpine environments, often dominated by plants with cushion growth forms, and show that community-level diversity is in most cases increased by facilitation, even in some alpine systems with dominant negative interactions measured at the patch level. Indeed, if nurse species add to the community species which are never present in open areas due to their high-stress- or disturbance-intolerance, the number of species of the whole community (cushions + open areas) will be increased by the presence of the nurses. Additionally, they show that this effect is even stronger in alpine systems with impoverished local diversity, suggesting that facilitation acts as an insurance policy in harsh alpine environments. This study highlights the importance of scale in facilitation studies, in particular in patchy ecosystems, which are very frequent in arid environments (e.g. Tewksbury & Lloyd 2001).

In another paper, Bräthen & Lortie (2016) show the important contribution of facilitation to diversity depending on shrub height in arctic tundra. Across a wide gradient of biomass (11–800 g m⁻²), including communities from both highly stressed and relatively benign arctic conditions, they observed in Norway a humped-back species richness/biomass relationship consistent with community theory and empirical studies (Grime 1973; Michalet *et al.* 2002; Fraser *et al.* 2015). Increasing shrub height significantly increased species richness all along the gradient, showing that facilitation by shrub canopies occurs in both stressful and competitive conditions. This result is novel because facilitation theory proposed that facilitation should contribute to shaping the humped-back species

richness/biomass curve only in intermediate to high stressful conditions but not in both benign and extremely stressful conditions where facilitation is absent or very weak (Michalet *et al.* 2006). Additionally, the positive or negative effect of community biomass for species richness is expected to be mediated by changing neighbour height along the gradient. In other words, the tallest neighbours should have a negative effect on species richness in benign environmental conditions, whereas mid-sized neighbours should have a positive effect on species richness at mid-position along the gradient. Finally, in extremely stressful conditions, these positive effects should collapse because neighbours become too short and too weak to have any positive effect on other species (Le Bagousse-Pinguet *et al.* 2014b). Although precise experimental comparisons with other systems are needed, these interesting results found by Bräthen & Lortie (2016) suggest that the role of facilitation for community diversity might be more ubiquitous than originally thought as argued by McIntire & Fajardo (2014).

However, changes in physical conditions induced by the facilitator species can have strong indirect effects for the dependent species, that is indirect interactions that could overwhelm the direct effect on diversity (see also Levine 1999; Michalet *et al.* 2015a,b). Building on the facilitation-expanded niche model proposed by Bruno, Stachowicz & Bertness (2003), Bulleri *et al.* (2016) explore the direct and indirect roles of facilitation in shaping community structure in both marine and terrestrial communities. In particular, they suggest that the broadening of niches by facilitation has the potential to increase overlap among potential competitors, with strong implications for the net effects of facilitation on species diversity. They show that the net effect of the facilitator species on realized species diversity will depend on a trade-off between fundamental species niche expansion and increased overlap among competitors and predators that determine the intensity of dependent species interactions. Additionally, they assess the consequences of niche-broadening influence of facilitation for species responses to climate change and ecosystem responses to changing diversity.

Facilitated species may also have negative effects on their benefactors. Feedback effects were poorly addressed in pioneer facilitation studies (but see Pugnaire, Haase & Puigdefábregas 1996), but following the 2009 BES meeting and its call for assessing the evolutionary consequences of facilitation (Bronstein 2009), several beneficiary feedback effects studies have been conducted in alpine environments (Michalet *et al.* 2011; Schöb *et al.* 2014a,b,c). Most of them found dominant negative feedback effects. In this Issue, Michalet *et al.* (2016) assess the importance of the functional composition of dependent species for these feedback effects. Using the alpine cushion data base of Butterfield *et al.* (2013), Cavieres *et al.* (2014) and Schöb *et al.* (2014a,b), and an additional survey in north-western China, they show that communities dominated by grasses have higher negative feedback effects than communities

dominated by forbs and legumes. Additionally, they show that the strength of the grass negative effect is stronger in dry alpine sites than in more mesic alpine sites. The results and ideas of Bulleri *et al.* (2016) and Michalet *et al.* (2016) may suggest that facilitative changes in physical conditions induced by a facilitator and the subsequent broadening of dependent species niches (*sensu* Bulleri *et al.* 2016) have the potential to also affect the fitness of the facilitator through the indirect facilitation of grass species with stronger negative feedback effects than forbs or legumes (*sensu* Michalet *et al.* 2016). All this complex network of indirect and feedback effects has the potential to affect selective pressures on the facilitator species and ultimately the eco-evolutionary stability of the whole interaction network (Bascompte, Jordano & Olesen 2006; Whitham *et al.* 2006; Bronstein 2009; Michalet *et al.* 2011).

Implications for ecosystem functions and services

Kéfi, Holmgren & Scheffer (2016) focus on the emergence of alternative stable states at community level in response to feedback interactions between or among organisms, a connection rarely addressed in the literature on facilitation in plant and animal communities. Kéfi, Holmgren & Scheffer (2016) address this gap, asking when positive interactions may lead to alternative stable states, and hence set the stage for catastrophic transitions at tipping points in ecosystems. They conclude that getting a clearer understanding of the links between species-level facilitation and ecosystem-level catastrophic shifts may depend on investigating whole networks of interactions between species and their abiotic environment, that is on merging ecosystem and community approaches. Therefore, there is still a need for a further integration of facilitation into ecological theory, more than a decade after the call by Bruno, Stachowicz & Bertness (2003). A better understanding of the role of facilitation could be essential for smart ecosystem management (and in particular, the prevention of catastrophic shifts) and ecosystem restoration (the better use of facilitation to trigger positive feedback loops).

Knowledge on facilitative plant–plant interactions is used by Brooker *et al.* (2016) in the final paper of this Issue to address an emerging problem derived from agricultural intensification, reductions in farmland biodiversity. Ecological knowledge applied to agriculture may enable biodiversity conservation in farmlands whilst addressing the pressing problem of food security. Obvious examples are intercropping systems, where combinations of crop species can – under some circumstances – allow reduced inputs of agrochemicals (fertilizers, pesticides) per unit yield, with potential knock-on benefits for biodiversity conservation. Other facilitative processes can also play a role in biodiversity conservation. Increased crop genetic diversity can help protect crops from pests and diseases. Although overlooked in facilitation research, Brooker *et al.* (2016) argue that the mechanisms involved operate

in analogous manner to associational defence against herbivores, a process well recognized in the facilitation literature. As with intercropping, many benefits to nature conservation can arise from reduced pesticide use per unit harvested crop. Our new understanding of facilitative processes arising from work on crop systems has lessons for the study of facilitative interactions in natural and semi-natural communities. Brooker *et al.* (2016) argue that some of the facilitative processes that are easy to identify and quantify in crop systems have been overlooked in non-crop systems and certainly deserve further consideration. They emphasize that new ecological understanding might deliver more sustainable agricultural practices.

Conclusions and future directions

This Special Feature is far from being a fully comprehensive overview of the numerous underlying mechanisms and community and ecosystem implications of facilitation. Other relevant topics are, for example, the phylogenetic and evolutionary consequences of facilitation or indirect interactions among plants, two current hot research areas (e.g. Butterfield *et al.* 2013; Al Hayek *et al.* 2015; Michalet *et al.* 2015a,b). However, we believe that this Special Feature provides evidence that focusing on underlying mechanisms and implications of facilitation certainly improved our knowledge on the importance of this fundamental process in ecological science. This knowledge even sheds light on patterns of variation in interactions along environmental gradients, a topic which historically has dominated, sometimes excessively, the literature on facilitation. For example, the first two papers on underlying mechanisms of facilitation showed through modelling and comparative empirical studies the incredible complexity of variation in facilitation along aridity gradients and their high dependency on the types of climate and soil moisture data. The two other papers of this first section of the Issue revealed two poorly assessed aspects of facilitation research, the relation with other trophic levels, below-ground with micro-organisms and in general with animals. The two-first papers of the second section of this Issue (community implications) showed two poorly known positive implications of facilitation for species diversity, community-level diversity and the ubiquity of this effect in some ecosystem types. In contrast, the two last papers of the second section highlighted two negative consequences of facilitation for diversity or the nurse fitness, either through niche-broadening processes and indirect interactions among beneficiary species or through beneficiary feedback effects. Finally, the two last papers of the Issue showed how facilitation may play a crucial role in driving critical transitions in ecosystem dynamics and contribute to improving the sustainability and efficiency of agriculture in a greener world.

Twenty years after the emergence of facilitation as an important modern research area, this Issue shows its high vitality and potential. We suggest that future studies should amplify the current focus on evolutionary conse-

quences of facilitation and indirect interactions among facilitated species, in particular addressing their likely interactions. The contribution of facilitation to the relationships between regional and local diversities also deserves to be further analysed (e.g. Michalet *et al.* 2015c). New important efforts should also be invested towards the relationship with below-ground organisms and other trophic levels, in particular through the use of network analyses. Finally, we certainly need to improve our knowledge on the mediating role of facilitation for community and species responses to climate change, a topic of crucial interest where our knowledge is still in its infancy (but see Brooker 2006; Anthelme, Cavieres & Dangles 2014).

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