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Meeting report

Is the cask of facilitation ready for bottling? A symposium on the connectivity and future directions of positive plant interactions

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The 2009 British Ecological Society's Annual Symposium entitled 'Facilitation in Plant Communities' was held at the University of Aberdeen, Scotland, from 20 to 22 April 2009. This was the first ever international meeting dedicated to the rapidly expanding field of facilitation. The aim of the symposium was to assess the current 'state-of-play' by contrasting findings from different systems and by looking outwards in an attempt to integrate this field with other related fields. It was also aimed at understanding how knowledge of facilitation can help understand community dynamics and be applied to ecosystem restoration. The symposium identified several key areas where future work is likely to be most profitable.

Keywords: community; competition; evolution; mutualism; positive interactions; restoration

1. AN INTRODUCTION TO FACILITATION

Twenty years ago, the term 'facilitation' would have made most ecologists think only of animal co-operation or plant community succession, although publications in the late 1980s had started to address the role of positive, non-trophic interactions in the succession of plant communities (e.g. Morris & Wood 1989). Accordingly, only 27 articles, including just five referring to plants, can be retrieved in the Web of Science database (ecology and plant sciences) using the keyword 'facilitation' for the 1900–1989 period; less than 2 per cent of those retrieved with the term 'competition'. In the last 20 years, a further 1252 publications have made some reference to facilitation, which represents close to 10 per cent of the volume that relates to competition. This clearly illustrates both the recent efforts made to clarify the role of facilitation, defined as 'species interactions that benefit at least one of the participants and cause harm to neither', and to incorporate it into mainstream ecological theory (Bruno *et al*. 2003; Lortie *et al*. 2004). In an overview of the topic, Callaway described how positive plant–plant interactions influence processes controlling the structure and function of plant communities and highlighted their role in important environmental issues including the relationship between biodiversity and ecosystem function, the impacts of global change and biological invasions and the evolutionary relationships among plants.

2. REFINING THE CONCEPT OF FACILITATION

The majority of presenters at the symposium would feel comfortable defining facilitation as the process by which an individual accrues a measurable fitness increase by the presence of another individual within the same trophic level. However, there was some lively debate around this point, in particular, relating to the similarities and differences between facilitation and mutualism and also considering the role of indirect interactions, e.g. facilitation mediated through other trophic levels. Mutualism is best conceptualized as interactions with positive effects for both interaction partners, and work in this field has had a focus on evolution or coevolution over time (Bronstein 1994; Stachowicz 2001). While several authors have already suggested future directions for facilitation research (e.g. Dodds 1997; Callaway 1998; Brooker *et al*. 2005; Maestre *et al*. 2009), none have done so with reference to the extensive body of mutualism research. By considering similarities and differences between mutualistic interactions (and research in the mutualism field), facilitation research can become more inclusive and begin to address topics such as the identification of key traits, specificity of facilitation and factors that lead to the reduction in facilitation. This provides a broad set of opportunities to explore the strength of the concept of facilitation not just in the context of a given interaction between individuals of two species at the same trophic level, but at a broader (evolutionary) time scale, including multi-trophic interactions.

Numerous opportunities were highlighted along these lines by van der Putten, including an increased focus on below-ground interactions, which may either mediate the outcome of plant–plant interactions or provide indications of the mechanisms associated with facilitation. Facilitation may also be prevalent within the marine environment both in inter- and subtidal environments. Bulleri showed how the marine ecology literature examines interactions in both sets of environments, but does not exploit the conceptual tools and hypotheses provided by the facilitation literature. This can potentially hinder understanding of these marine systems and also slows the search for generalities through the testing of hypotheses across a broad range of systems. Lost opportunities for connection to other subdisciplines and hypotheses even within ecology will continue to prevail unless the application of

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definitions is appropriately clarified—specific and precise where needed, but sufficiently broad and general for researchers to be able to readily identify linkages.

3. EVOLUTIONARY PERSPECTIVES: LESSONS FROM MUTUALISM

It has already been suggested that considerable progress might be made by considering the evolutionary aspects of facilitation (Brooker *et al.* 2008). The need for an evolutionary perspective was reinforced during this meeting, and several concrete areas for future research activity were identified. Bronstein identified five focal areas of mutualism research that may be helpful for designing studies of the role of facilitation in community evolution: (i) the evolutionary origins and maintenance of the interaction; (ii) trait evolution; (iii) the continuum from specialization to generalization; (iv) coevolution of partners; and (v) the existence of cheating on the interaction. She also stressed that a necessary future step for understanding the evolutionary dynamics of facilitation will be to identify effects from the perspectives of both partners in the interaction. In contrast to mutualism, in most cases of facilitation, the effects of the beneficiary species on the benefactors are unknown, although community genetics studies have documented the occurrence of such feedbacks across trophic levels (e.g. Whitham *et al.* 2006). They may be positive, negative or neutral, and their assessment among plants remains to be addressed.

By integrating biogeographic, paleobotanical and ecological information, Valiente-Banuet showed how facilitation is a source of stabilizing selection for the regeneration niches of ancient tertiary species within Mediterranean-climate ecosystems. He presented evidence that these positive interactions have preserved global diversity throughout evolutionary time, demonstrating that facilitation is not just a transient process. Such maintenance of positive interactions throughout evolutionary time is an important premise for expecting facilitation to drive community evolution. Brian Kopach used trait measurements and experiments to show that facilitation rarely weakens the selection pressures imposed by the abiotic environment. This work suggests that facilitation may not be strong enough to overcome abiotic selection to increase the range size of species.

4. COMMUNITY-LEVEL EFFECTS AND ECOSYSTEM RESTORATION

Several talks in the symposium emphasized that facilitation raises diversity not only at the level of species, but also at the genera and family level (Cavieres). Also, facilitative effects can propagate from relatively minor components of the ecosystem, such as parasitic plants (Watson), and impact higher trophic levels (Holmgren & Bulleri).

If major plant–plant interactions can be identified, then restoration schemes can be modified to take this knowledge into account. A meta-analysis of woodland restoration studies by Gómez-Aparicio indicated that, in general, herbs had negative effects on tree establishment and survival, whereas shrubs had positive effects. This knowledge can be used to improve prescriptions and methods. Modelling studies indicate that the behaviour of the 'host' species (the dominant benefactor of the community) can drive the rest of the system but that the impacts may differ between extreme environments, where positive feedbacks between species predominate, and less severe environments with much higher incidences of negative interactions between species (Butterfield).

The conclusions from a number of papers and the general discussions identified a number of areas where significant advances could be made. Experiments and field studies increase our understanding of how facilitation may dampen or amplify community responses to disturbance and environmental change. This should progress in parallel with modelling studies that, by including plant functional traits, can make predictions concerning how species may interact along environmental gradients (Sutherst *et al.* 2007). Similarly, identification of the traits of nurse plants will go a long way to improving restoration schemes by encouraging plant establishment and survival. These advances would help tie facilitation into other areas of ecology.

5. FUTURE DIRECTIONS

The general feeling of the meeting was that sufficient research had been carried out in the last 15 years to make initial attempts at synthesis worthwhile and to identify fruitful future research directions. Discussion distilled this into four areas:

(i) Semantics matter and a clear definition of what constitutes facilitation is required if the field is to communicate successfully with other related areas of ecological and evolutionary research. It needs to be decided whether it is facilitation only when a positive interaction occurs between members of the same trophic level. Other trophic levels may then be important in driving indirect facilitation, in the same way that apparent competition is mediated by shared predators. We need to be clear about the relationship with mutualism: are some mutualisms also facilitation and vice versa?

(ii) Facilitation has been seen as a short-term, transitory interaction, but if there are costs or benefits to one or both partners, then there is material on which natural selection can work. Consequently, there is a promising avenue for new research assessing the role of facilitation in evolution and identifying key response and effect traits on which selection acts.

(iii) If evolution has shaped positive interactions between plants, we need to understand it better, in order to help conserve the patterns of diversity we observe in different environments. We may also learn much from studying the development of interactions without any evolutionary history, such as those occurring between native and invasive plants (Reinhart *et al.* 2006).

(iv) Finally, if we understand how different traits are related to benefactors and beneficiaries,

then we can screen communities for these potential response and effect traits and, hopefully, make predictions concerning their stability in the light of environmental change. This will help to improve our theoretical and practical knowledge of how communities assemble, react to change and can be restored.

The papers from this symposium will be published in a special online edition of the *Journal of Ecology*, with an introductory paper published in the main journal.

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