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Is Facilitation a True Species Interaction?

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Abstract: Current ecological literature considers facilitation to be a positive interaction alongside symbiosis or mutualism. But unlike these interactions, the fitness of one of the species involved in facilitation remains unaffected which precludes coevolution. Therefore, we believe that facilitation is not a true species interaction and should be kept within the framework of succession.

INTRODUCTION

For the past few decades, ecologists have demanded a greater presence of positive interactions in ecological theory (e.g. Risch and Boucher 1976, Boucher *et al.*, 1982, Bronstein 1994, Bruno *et al.*, 2003). According to these claims, positive interactions could be as important as competition and predation in determining the structure of ecological communities (see also Stachowicz 2001). However, it seems that the scientific community is not responding. More than 30 years ago, Risch and Boucher (1976) counted 362 papers on competition, 321 papers on predation, and 35 papers addressing mutualisms. May and Seger (1986, cited by Peters 1991) found similar ratios of competition, predation, and mutualism studies, both in articles published in ecological journals (4:4:1 respectively) and in the numbers of pages in ecological textbooks (5:6:1 respectively). We would like to open a discussion of why there is a lack of studies focusing on one particular positive interaction, facilitation, by first delimiting what positive interactions are, defining facilitation, and then analyzing the ecological and evolutionary consequences of species interactions.

Some authors argue that competition and predation have traditionally dominated the ecological literature as a reflection of prevailing social ideas in western societies (where most ecologists are educated) during the 20th century (see for example Boucher *et al.*, 1982). Unlike predation, which can be easily observed and measured, both competition and positive interactions, such as mutualism or symbiosis, are elusive and difficult to quantify (McIntosh 1987, Peters 1991; see conflict in definitions by Wilkinson 2001). Moreover, while predation has an unambiguous effect on the fitness of consumed prey, competition and positive interactions typically have subtle or indirect consequences such as changes in growth or fecundity (Holt 1984, Peters 1991). Therefore, the deficit in positive interaction articles may be explained by inherent difficulties in studying ambiguous effects of such interactions.

Alternatively, the reason for the low proportion of studies on positive interactions could be the ambiguity of some definitions (e.g. Wilkinson 2001, Hodges 2008). Ecological interactions occur between individuals of two species, and are commonly represented by a combination of symbols representing whether the outcome for each individual is positive (+) or negative (-). Thus predation and parasitism are represented as [+,-], competition as [-,-] and symbiosis and mutualism as [+,+]. More problematic is the definition of interactions that are irrelevant to one of the species involved. For example, in facilitation [+ , 0], commensalism [+ , 0] and amensalism [- , 0], individuals of one species are unaffected by the interaction. In such a relationship, can the unaffected individual really be considered as interacting with the “+” or “-” organism? In other words, are facilitation, commensalism and amensalism true species interactions?

DEFINITIONS AND USES OF FACILITATION

It is interesting to note that facilitation was not included in the list of positive interactions thirty years ago but instead was a concept within successional theory (Risch and Boucher 1976, Boucher *et al.*, 1982). However, over the years facilitation gained attention as a potential interaction between two species and concepts overlapped. Of all positive interactions we have found facilitation to show the most conflict in definition, due to at least two different uses of the term. Facilitation has been used to describe community formation and succession, where a species facilitates a habitat for new incoming species (e.g. Connell and Slatyer 1977). The term has also been used to encompass all non-negative species interactions, i.e. those in which at least one species benefits and neither is negatively affected (e.g. Krebs 2001, Stachowicz 2001, Bruno *et al.* 2003). Within such framework we see concepts such as ecosystem engineers (Flecker 1996, Coleman and Williams 2002), where a single species can alter habitat and affect the presence of one or more coexisting species. Clearly, the uses of facilitation, whether as a community property or specific species interaction, can be confusing and have been used interchangeably. Here we argue that facilitation is not a true interaction between two species and should be kept within the framework of succession.

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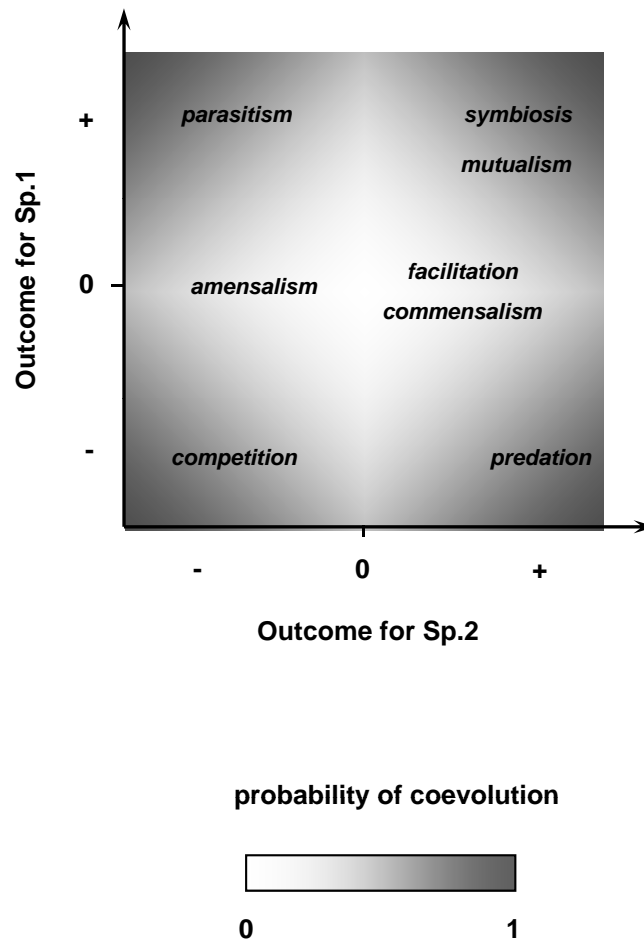


Fig. (1). Landscape of ecological interactions and their potential as a force promoting coevolution. The axes indicate the outcome of the interaction for each of the two species involved, which can be negative, neutral or positive. The grey gradient reflects the likelihood of coevolution between the two species as a consequence of their interaction. Interactions that fall on the white area can promote evolutionary changes in one of the species but not coevolution.

Further complicating the use of facilitation to describe a species interaction is the term commensalism, which by definition also describes a $[+, 0]$ relationship but focuses specifically on food acquisition by the “+” species (Lincoln *et al.*, 1998). There is debate as to whether any commensal relationship is truly without effect on one species or instead is better described as mutualism or parasitism (Strong 1983, Toft and Karter 1990). In this respect, observations of commensalism could simply be the result of difficulties in identifying effects of the interaction on the “0” species. The same limitation may be applicable in studies identifying interactions as facilitation (but see Bruno *et al.*, 2003).

TRUE INTERACTIONS AFFECT EVOLUTIONARY TRAJECTORIES OF INTERACTING SPECIES

We believe that an evolutionary perspective could help clarify inconsistent definitions of some positive interactions. Interaction between two species tends to produce coevolution (Thompson 1988) as a consequence of changes in the fitness of both species (Fig. 1). For example, arms races between predators and prey result in changes to both species (e.g. Brodie and Brodie 1999). The same occurs between competitors (Connell 1980), mutualists (Schmitt and

Holbrook 2003) or symbionts (Baker 2003). All of the above interactions use positive or negative symbols for both species involved (the grey area of Fig. 1). Ecological theory has made clear how these interactions have considerable consequences over evolutionary time, either shaping niche space (Chase and Leibold 2004) or intrinsic species properties (Thompson 1988). For interactions with a “0” component, the unaffected species’ fitness does not change due to the interaction and thus there is no evolutionary pressure to coevolve (white area, Fig. 1). Therefore we believe that interactions with no effect on one species should not be considered as true species interactions. Based on this idea, we can include the concept of fitness and define facilitation as: The act of one species (facilitating species) providing a means to enhance the survivorship/fitness of another species, without impacting the fitness of the facilitating species. Facilitation is not an interaction regardless of the benefits obtained by a single species; by this definition commensalism is a specific type of facilitation. Lincoln *et al.*, (1998) define commensalism as a “symbiosis in which one species derives benefit from a common food supply whilst the other species is not adversely affected”.

In conclusion, facilitation is a process affecting community dynamics and succession, and the term should not be

used within the parameters of positive interactions. Differentiating facilitation from positive interactions will reduce confusion and aid conceptual, theoretical and empirical work concerning positive interactions (e.g. Hodges 2008). Positive interactions are either underrepresented in nature or in the literature, and determining which of these two cases exists should be the direction of future research. The first step towards this goal is to understand what positive interactions are and the subtle differences among them (Fig. 1). We believe that a key principle for evaluating species interactions is the potential for coevolution. Regardless of the disparate evolutionary implications of positive interactions, we do not deny their role in structuring ecological communities and determining the distribution and abundance of species. However, given the arguments above, we conclude that [+ , 0] relationships such as facilitation are not true species interactions, and that this distinction may explain the apparent lack of positive interactions in nature.

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