

Do indirect interactions always contribute to net indirect facilitation?



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ABSTRACT

Indirect facilitation theory assumes that the addition of species in complex communities should decrease competitive interactions through the emergence of positive indirect effects among competitors. However, experiments conducted in communities have rarely observed a net indirect facilitation. We hypothesize that this may be due to the likely occurrence of negative indirect interactions that were overlooked in indirect facilitation theory. We used a spatially explicit modeling approach to quantify indirect effects and net interactions occurring within a system of three competitors. In contrast to field experiments our modeling approach allows quantifying positive indirect effects since their calculation needs to be done in absence of direct negative effects. We showed the existence in a system of three competitors of two negative indirect interactions, in addition to the positive one emphasized in indirect facilitation theory. We also made precise the conditions under which the balance of these three indirect interactions becomes negative and induces a competition enhancement and in turn no net indirect facilitation. The existence of negative indirect effects among competitors contributes to explain the rare occurrence of indirect facilitation in plant communities.

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1. Introduction

Indirect facilitation has been defined as a positive interaction occurring between two species in complex communities through the mediation of at least an intermediate species, such as herbivores, pollinators, mycorrhizal fungi, soil microbes, or other competing plant species in the case of plant communities (Callaway, 2007). Indirect facilitation has been proposed as a potential mechanism for explaining the maintenance of diversity in complex communities subjected to high levels of pair-wise competitive interactions (Levine, 1976, 1999; Miller, 1994; Callaway, 2007; Brooker et al., 2008; Allesina and Levine, 2011). However, a number of studies have shown that indirect facilitation may also contribute to community invasion (Siemann and Rogers, 2003; Saccone et al., 2010).

Early indirect facilitation studies have mainly explored its role in complex communities using models (Levine, 1976; Lawlor, 1979; Higashi and Patten, 1989; Vandermeer, 1990; Stone and Roberts, 1991). Fath (2007) showed that community-level relations usually have a greater occurrence of mutualism than competition making them more positive than the direct relations that produced

them. More recently a number of experiments have been conducted to determine the mechanisms driving its occurrence in plant communities. Two main interactive systems were studied, either two competing plant species with a herbivore (Rousset and Lepart, 2000; Brooker et al., 2006; Smit et al., 2007; Vandenberghe et al., 2008; Anthelme and Michalet, 2009) or three competing plant species (Levine, 1999; Callaway and Pennings, 2000; Pagès et al., 2003; Pagès and Michalet, 2003, 2006; Siemann and Rogers, 2003; Dormann and Roxburgh, 2005; Kunstler et al., 2006; Callaway and Howard, 2007; Weigelt et al., 2007; Cuesta et al., 2010; Saccone et al., 2010).

Levine (1976) proposed that indirect facilitation (i.e., the net positive effect on a target species C) may occur in both interactive systems only when the indirect positive effect of a species A on C, due to a decrease in the competitive or predation effect of a species B on C (competition or predation release, respectively, induced by the competition effect of A on B), is not overwhelmed by the direct negative effect of A on C (Fig. 1). Additionally, Levine (1999) proposed that the three competing species should compete for different resources (e.g., light and water or nutrient) or for different mechanisms (e.g., resource competition and interference or allelopathy). For example, Kunstler et al. (2006) showed in shrubby grasslands of the French Central Massif that shrubs (A) indirectly facilitate tree seedlings (C) through a competitive release of grasses (B) on tree seedlings, because shrubs inhibited grasses for light while grasses competed with tree seedlings for water. Similarly, Saccone et al. (2010) showed that adults of the invasive

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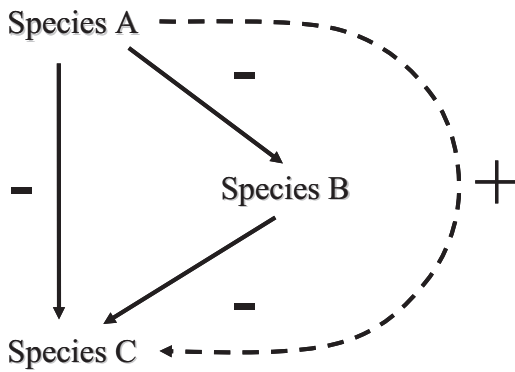


Fig. 1. The indirect facilitation model in a network of three competitors A, B and C. The solid arrows indicate direct negative interactions. The dashed arrow represents the net positive effect (indirect facilitation) for the target species C.

Acer negundo indirectly facilitated their own seedlings in European floodplains by shading exploitative forest weeds competing with *Acer* seedlings for nutrients.

However, in most of these experiments the net positive effect for the target species is generally weak and a number of authors have even found either no significant net effect (Levine (1999) for two of three target species, Kunstler et al. (2006) for one of two targets and Saccone et al. (2010) for three of four targets) or even an increase in competition for the target species, as shown by Pagès and Michalet (2003, 2006) and Pagès et al. (2003) for five target species in forest communities. Pagès et al. (2003) argued that the net effect was not significant or even negative for the target species in forest communities because the direct negative effect of adult trees on the target (due to shade) overwhelmed the positive indirect effect (due to increasing nutrient availability).

Another hypothesis potentially explaining the rare occurrence of indirect facilitation in complex communities or the weakness of the effect for target species may be due to the occurrence of indirect negative interactions beside the well-emphasized positive indirect interaction. Negative indirect interactions have been shown to exist in animal communities and have been defined as ‘apparent competition’ (Holt, 1977), ‘trait-mediated indirect interaction’ (Werner, 1992; Abrams et al., 1996) or ‘interaction modification’ (Wootton, 1993). In contrast, studies conducted in plant communities have

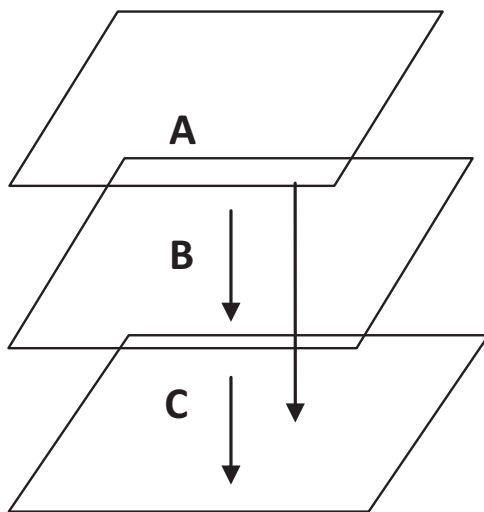


Fig. 2. The three overlapping lattices of the modeled community composed of species A, B and C. The arrows indicate the directions of competitive effects among species.

only considered the occurrence of indirect positive interactions (competition or predation release).

However, the experimental assessment of this hypothesis is quite difficult in natural communities, since the measurement of the indirect interaction occurring between species A and C should be done in absence of direct interaction between those two species. Thus, an efficient way to assess if negative indirect interactions exist in a system of three competitors is certainly through modeling, because models may allow us exploring the full range of interactions among species, including conditions where direct interactions are null.

The main objective of our study is to assess with an individual-based spatially explicit simulation model the potential occurrence of indirect negative interactions in a network of three competing species. Additionally, if negative indirect interactions exist, we aim to analyze the conditions under which they may contribute to produce a net negative effect for the target species, likely to explain the rarity or weakness of net indirect facilitation found in plant communities.

2. Methods

2.1. Parameters of the model and quantification of direct interactions

In our model, the community is composed of three species A, B and C, which live in different overlapping lattices with the same size (100×100 cells, Fig. 2). For the three lattices each cell is either empty or occupied by only one species individual. The species from the upper lattices have a competitive effect on the species from the lower lattices, but not vice versa. Thus, there is only a competitive effect of A on both B and C, and a competitive effect of B on C. In our model competition affects species’ survival rate. Therefore, species survival rates are:

$$A : S_A = S_{max} \quad (1)$$

$$B : S_B = S_{max} \quad \text{without A above} \quad (2)$$

$$S_B = S_{max} - C_{AonB} \quad \text{with A above} \quad (3)$$

$$C : S_C = S_{max} \quad \text{without A and B above} \quad (4)$$

$$S_C = S_{max} - C_{BonC} \quad \text{without A but with B above} \quad (5)$$

$$S_C = S_{max} - C_{AonC} \quad \text{with A but without B above} \quad (6)$$

$$S_C = S_{max} - C_{AonC} - C_{BonC} \quad \text{with both A and B above.} \quad (7)$$

C_{AonB} , C_{AonC} , C_{BonC} are indices of interaction strength (Wootton, 1994) or per-capita negative effects of A on B, A on C and B on C, respectively. These indices have increasing positive values with increasing competition intensity. S_{max} is the maximum survival rate and we assume S_{max} is the same for all species. S_A , S_B and S_C values range from 0 to 1.

At each time step all individuals within the community experience a death process with a survival probability of S_A , S_B and S_C for species A, B and C, respectively. The survivors reproduce and disperse their propagules. When reproduction occurs, an individual produces propagules that are identical to its parents. Each propagule is dispersed randomly to any cell within its own lattice, and the propagules can only invade the empty cells. The total number of these propagules for each individual equals to r , and we assume r is the same for all species.

All simulations were started with saturated communities such as each species occupies all the cells of its own lattice (10,000

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