Beyond dual-lattice models: Incorporating plant strategies when modeling the interplay between facilitation and competition along environmental severity gradients

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ABSTRACT

We introduce a spatially explicit model that evaluates how the trade-offs between the life strategies of two interacting plant species affect the outcome of their interaction along environmental severity gradients. In our model, we represent the landscape as a two-dimensional lattice, with environmental severity increasing from left to right. Two species with different strategies, a competitor and a stress-tolerant, interact in the lattice. We find that facilitation expands the realized niche of the competitor into harsh environments by suppressing the stress-tolerant species. Most of their coexisting range is dominated by a positive effect of one species on another, with a reciprocal negative effect from the species receiving the benefits on its benefactor ("+, −"), whereas mutualistic ("+, +") interactions are only found in the harshest part of the environmental gradient. Contrarily as assumed by models commonly used in facilitation research (e.g. dual-lattice models), our results indicate that "+, +" interactions are not dominant, and that their differences with "+, −" interactions along environmental severity gradients depend on the strategies of the interacting species. By integrating the trade-off between competitive ability and stress tolerance, our model provides a new framework to investigate the interplay of facilitative and competitive interactions along environmental gradients and their impacts on processes such as population dynamics and community organization.

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1. Introduction

The study of intra- and inter-specific interactions between plant species and their implications for ecosystem structure, functioning and dynamics has been an important ecological research theme for decades (Clements, 1929; Oosting, 1956; Keddy, 1989; Callaway, 2007). Among these interactions, the study of facilitative or positive interactions has occupied a prevalent place, especially during the last twenty years (see Brooker et al., 2008 for a recent review). Their importance for maintaining ecosystem structure and functioning in a wide range of terrestrial ecosystems is now widely acknowledged, as studies have shown how positive interactions can promote plant species growth and reduce mortality (Bertness and Leonard, 1997; Maestre et al., 2001; Callaway et al., 2002), influence ecosystem structure (Tirado and Pugnaire, 2005; Valiente-Banuet and Verdú, 2007), and affect ecosystem functioning (Mulder et al., 2004).

Most of our knowledge on this important topic was generated from empirical field studies (as argued by Callaway, 2007; Brooker et al., 2008). While these studies are useful for understanding the importance of positive interactions in nature, and the mechanisms underlying them, they are of limited utility to evaluate their impacts on aspects such as population dynamics, evolutionary processes and ecosystem functioning at the long term (but see Valiente-Banuet and Verdú, 2007, 2008). To overcome some of these limitations, mathematical and computer models are increasingly being used in facilitation research (Matsuda, 1987; Taylor, 1992; Wilson et al., 1992; Yamamura et al., 2004; Zavala and Bravo de la Parra, 2005; Travis et al., 2005, 2006; Brooker et al., 2006). Among the models proposed, the dual-lattice model introduced by Doebeli and Knowlton (1998), and further developed by Yamamura et al. (2004), has received increased attention. This model has been successfully employed to study the interplay of facilitative and competitive interactions along environmental gradients (Travis et al., 2005, 2006), and to evaluate the joint impacts of biotic interactions and environmental factors on the distribution of species (Brooker et al., 2006).

Although dual-lattice models can provide important insights on the mechanisms driving biotic interactions, and on their

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dynamics along environmental gradients, they do not consider facilitation in the same way as most empirical plant ecologists would understand it. (Brooker et al., 2008). These models represent positive interactions as mutualistic ("+, +"), which is just one of the potential outcomes of a pairwise interaction; facilitation may also occur in concert with negative ("+, −") or neutral ("+, 0") reciprocal responses from the beneficiary to the benefactor species (Callaway, 2007). Another drawback of dual-lattice models lies in the fact that they do not take into account the characteristics of the interacting species. In these models, the interacting species are totally identical with respect to each other. In the real world, however, co-occurring species differ in their stress tolerance and competitive ability (e.g. Campbell et al., 1992; Niinemets and Valladares, 2006), and these differences strongly impact the net outcome of biotic interactions (Choler et al., 2001; Liancourt et al., 2005; Wang et al., 2008). Therefore, incorporating trade-offs between the stress tolerance and competitive ability of the interacting species is crucial when studying the interplay of facilitative and competitive interactions along environmental severity gradients, and would represent a step ahead in the development of models to study biotic interactions.

Dual-lattice models consider that the interacting species live in separate lattices, a feature that makes them highly suitable for the study of mutualism, but that limits their application to study the interplay of competitive and facilitative interactions (Doebeli and Knowlton, 1998). It is well known that, regardless of their net outcome, species interactions comprise both negative and positive effects, and that their relative importance fluctuate with environmental conditions (Holzapfel and Mahall, 1999; Maestre et al., 2003). The beneficiary species compete with the benefactor for limiting resources such as water, nutrients and light, but at the same time may get benefits from it in the form of increased nutrient availability, improvements in microclimate or protection from browsing (Maestre et al., 2003; Callaway, 2007). This interplay of positive and negative interactions is not well considered in dual-lattice models. That is because they define facilitation by including a parameter indicating the positive effects of the benefactor on the beneficiary, but the competitive effects of benefactor on the beneficiary are not represented by any specific parameter (Travis et al., 2005, 2006). Another problem of these models is the division of the dual-lattice structure, which precludes any niche overlapping between interacting species because they live in separate lattices and compete for the different portions of space available. It has been shown that competitive interactions may exclude stress-tolerant species from communities when environmental severity is low (Grime, 1973, 1974, 1979; Michalet et al., 2006). But if the two interacting species "live" on different lattices, as represented in dual-lattice models, this competitive exclusion cannot take place. Therefore, these models do not represent inter-specific competition properly, making them not fully appropriate to investigate the variations in the relative importance of competition and facilitation along environmental severity gradients.

The above paragraphs present some of the limitations of models currently being employed in facilitation research, and highlight the need for new modeling approaches (Brooker et al., 2008). These should distinguish between mutualism and facilitation, accommodate variation in the role of facilitative interactions along environmental gradients, both in space and time, and take into account the competitive ability and stress tolerance of the interacting species, which may define the outcome of biotic interactions along such gradients (Choler et al., 2001; Liancourt et al., 2005). With this in mind, we developed a spatially explicit model that evaluates the effects of environmental severity on the spatio-temporal dynamics of interacting species differing in their competitive ability and stress tolerance. With this model, we

explore how the trade-off between these strategies will affect (i) the interplay between facilitative and competitive interactions along environmental severity gradients, (ii) the relationships between mutualism and facilitation, and (iii) the spatial distribution and coexisting range of the interacting species.

2. Materials and methods

2.1. The model

Two kinds of species interact in our model: a competitor and a stress-tolerant (*sensu* Grime, 1979). They are characterized by a low stress tolerance-high competitive ability and a high stress tolerance-low competitive ability, respectively (see Grime, 1979 for more characteristics of both strategies). Although it is unlikely that highly stress-tolerant and competitive species will co-exist in the same environment, we use this dichotomy to illustrate how differences in life history and physiology among co-existing species can influence the outcome of their interaction in a simplified manner.

In our model, we represent the landscape as a two-dimensional lattice. Each cell of the lattice can be empty, or be occupied by a single individual of only one species. We define the neighborhood as the Moore neighborhood, which includes the eight immediate neighbors of a given cell: north, northeast, east, southeast, south, southwest, west, and northwest (Ifti et al., 2004). We use a linear gradient to determine the quality of sites along the length of the lattice. Environmental severity increases from left to right; the environment is most benign at the left edge of the lattice, and the harshest conditions are found in the right edge of the lattice. The reproduction rate of both species, r, attains its maximum value (r_{max}) at the most benign environment, and is reduced to its minimum value (r_{min}) at the right edge of the lattice. We assume r varies linearly with environmental severity. Therefore, the reproductive rate r of the stress-tolerant species can be defined as:

$$r_{stress\text{-}tolerant} = r_{max} - (r_{max} - r_{min})S$$

where S indicates the degree of environmental severity; it equals to 0 and 1 at the left and right edges of the lattice, respectively.

When reproduction occurs, an individual produces propagules that are identical to the parents. The total number of these propagules equals to r. If the r value is not an integer, the decimal portion of r is compared to Q, a uniform random number on the $(0, 1)$ interval. If it is larger than Q, the total number of propagules equals to the integer portion of r plus one; otherwise, it equals to the integer portion of r. Each propagule is dispersed sequentially to one cell that is randomly selected from the cells in the parent's neighborhood. The propagules of the stress-tolerant species can only be established in an empty cell; therefore if there is a single propagule from a stress-tolerator and a single empty cell within a neighborhood, the propagule has a 1/8 probability of occupying the empty cell. Propagules of the competitive species, which can also occupy these cells, have a probability p to invade the cells occupied by the stress-tolerant species. Propagules of both species cannot be established in cells occupied by the same species. Therefore, p indicates the ability of competitive species to competitively exclude the tolerant species from its own occupied cells. However, the competitor is more susceptible to abiotic stress than the stress-tolerant species, i.e. there is a trade-off between the competitive ability and stress tolerance (Grime, 1973). We assume that the reproduction rate of competitive species declines more rapidly with the increase in environmental severity, and that this reduction is proportional to its competitive ability (p). Therefore, the reproductive rate of competitive species can be

defined as:

$$r_{competitor} = r_{max} - (r_{max} - r_{min})S/(1 - p)$$

where $0 \leqslant p < 1$. We consider $r_{competitor}$ to be zero when it becomes negative.

We also define a facilitation coefficient, f, which indicates a species' ability to ameliorate the abiotic stress within its neighborhood. In our model, we only consider inter-specific facilitation, which happens when there are other species existing within the target neighborhood and $f > 1$. Facilitative effects will ameliorate the environmental stress endured by the target species, and this amelioration will increase its reproduction rate (as is often found in harsh environments where facilitation is prevalent; Esler, 1999; Bruno et al., 2003; Tirado and Pugnaire, 2003; Callaway, 2007). In our model, facilitation happens at the level of the Moore neighborhood just like competition and dispersal, not at the level of the entire lattice. For simplicity, we assume that f is the same for both species, i.e. both of them have the same ability to ameliorate the abiotic stress experienced by the other one. The intensity of facilitative effects will increase with f. The reproductive rates of both species once facilitation is taken into account can be defined as:

$$r_{stress\text{-}tolerant} = r_{max} - (r_{max} - r_{min})S/f$$
$$r_{competitor} = r_{max} - (r_{max} - r_{min})S/(f(1 - p))$$

where $f \geqslant 1$; when $f = 1$, there is no facilitation.

All the lattices in our simulation are 200×200 cells in size. We take a "wraparound" (torus) approach to avoiding edge effects. Since the environment is most benign at the left edge of the lattice and is harshest at the right edge of the lattice, the wraparound is not conducted at the horizontal direction but only at the vertical direction (Travis et al., 2005, 2006). We use asynchronous updating that works in the following way. First a single individual is selected at random. Second, we determine whether it survives the probability of mortality (d). If it survives we calculate its probability of fecundity and it may reproduce and disperse propagules. Every time step is made up of N such updates, where N refers to the number of all individuals. Initially, both species are distributed randomly across the grid, and each occupies half of the total number of available cells (20 000). All the simulations were run for 2000 time steps in order to allow the system to reach a steady state (Fig. 1). The mean density for each value of S (i.e. the total number of cells occupied by each species divided by the total number of cells in each column of the lattice) was determined as the mean value of 500 time-steps after the 2000 startup steps in a single model run (Travis et al., 2005, 2006).

In order to explore the net outcome of competitive and facilitative interactions more thoroughly, we calculated the relative neighbor effect (RNE) index for the interacting species along the environmental severity gradient. This index is calculated as follows (Markham and Chanway, 1996):

$$RNE = (D_{T-N} - D_{T+N})/X$$

where D_{T-N} and D_{T+N} are the density of the target species in the absence and presence, respectively, of other species within the landscape, and X is the greater of the two. To facilitate interpretation of the results, we multiplied RNE values by -1 (Callaway et al., 2002; Maestre and Cortina, 2004). Positive values of RNE indicate that a species has a greater density in the presence of heterospecifics than in their absence, negative values of this index indicate the opposite, and $RNE = 0$ means that heterospecifics have no effect on the density of the target species.

We also evaluated the effects of different values of p and f on the net outcome of the interaction between the two species. In order to do this, we show how the distributive range of species' "+, +" and "+ −" interaction types along environmental severity
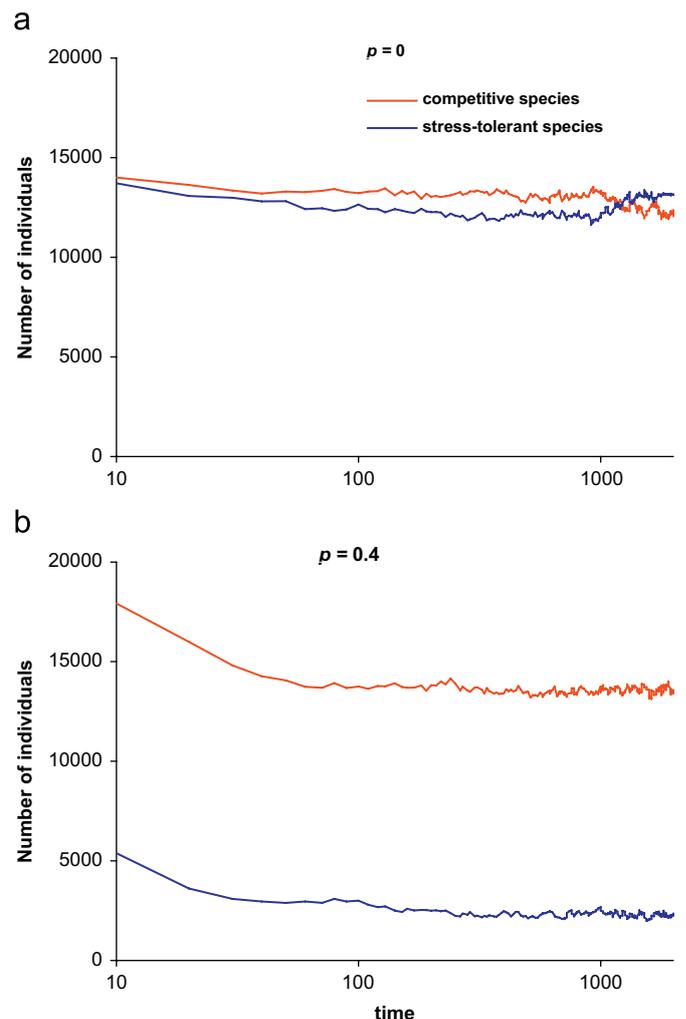

Fig. 1. Dynamics of the total number of individuals within the lattice through time when p is either 0 (a) or 0.4 (b). Blue and red lines indicate the stress-tolerant and competitive species, respectively. The parameter values used in the simulations were: $r_{max} = 1.0$, $r_{min} = 0.2$, $d = 0.2$ and $f = 3.5$. Note the log scale on the x-axis. (For interpretation of the references in to colour in the figure legend, the reader is referred to the web version of this article.)

gradients will change with the variations of f and p. Values of p are in the interval [0, 1), sampled in steps of 0.02, and those of f are in the interval [1, 6], sampled in steps of 0.1. We performed all the simulations in NetLogo (Wilensky, 1999), a powerful multi–agent modeling language which is particularly well suited for modeling complex systems developing over time.

3. Results

When two species are identical ($p = 0$), the realized niche (the distributive range of species along environmental severity gradients) of each species is the same as that occupied when they are living alone (Figs. 2a and b). When both are competing, there is no shrinking of the realized niche occupied by each of them, but their densities are substantially reduced (Fig. 2c). When facilitation is taken into account, there is an expansion of the realized niche occupied by both species, and their density substantially increases when moving along the environmental severity gradient (Fig. 2d).

When the competitive species is able to competitively exclude the tolerant species from its own occupied cells with a particular
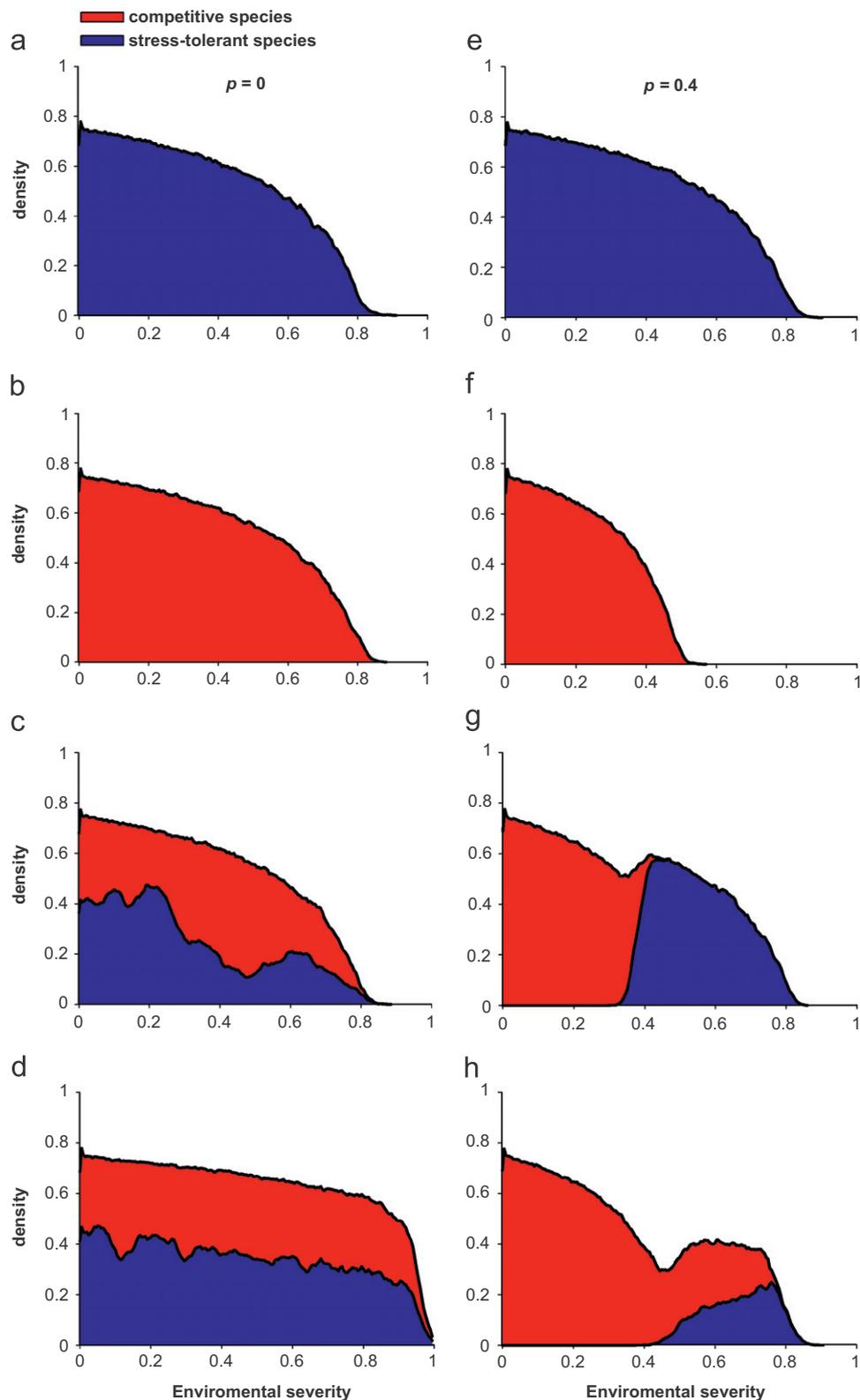
Fig. 2. Mean density of competitive (in red) and stress-tolerant (in blue) species along the environment severity gradient when $p = 0$ (left panels) and $p = 0.4$ (right panels). (a) and (e) Stress-tolerant species in the absence of cumpetitive species. (b) and (f) Competitive species in the absence of stress-tolerant species. (c) and (g) Stress-tolerant and competitive species together without facilitation. (d) and (h) Stress-tolerant and competitive species together with facilitation. The two species are identical with each other when $p = 0$. The parameter values used in the simulations were the same as those used in Fig. 1. (For interpretation of the references in to colour in the figure legend, the reader is referred to the web version of this article.)

probability ($p = 0.4$), there is a trade-off between the competitive ability and stress tolerance of the interacting species (Figs. 2(g) and (h)). When the two species live alone, the realized niche

occupied by the stress-tolerant is larger than that inhabited by the competitor (Figs. 2(e) and (f)). When both are competing, the realized niche occupied by the stress-tolerant is reduced more

than that inhabited by the competitor (Fig. 2(g)). When facilitation is taken into account (Fig. 2(h)), there is a large expansion of the realized niche occupied by the competitor, whereas both the realized niche occupied by the stress-tolerant and its density are substantially reduced.

When two species are identical ($p = 0$), the RNE values for both species will change from negative to positive concurrently with the increase in environmental severity. The net outcome of their interactions types will change from a negative ("– –") to a mutualistic ("+ +") interaction with the increase of environmental severity (Fig. 3a). When there is a trade-off between the competitive ability and stress tolerance ($p = 0.4$), the RNE values of the stress-tolerant also will change from negative to positive with the increase of environmental severity, but the range where they are positive is substantially reduced (Fig. 3b). When $p = 0.4$, the *RNE* for the competitor is either zero or positive, and will

achieve its maximum value at moderate levels of environmental severity. For this species, the net outcome of its interaction with the stress-tolerant will change from "+ –" to "+ +" with the increase of environmental severity within their coexisting range (Fig. 3b).

Interactions of the type "+ –" exist for most of the combinations of p and f evaluated (Fig. 4). The distributive range of this interaction along environmental severity gradients is much larger than that of a mutualistic interaction ("+, +") for a majority of these combinations. There is an increase in the distributive range of the mutualistic interaction type for the combinations of large f and small p values (Fig. 4a). The distributive range of the "+ –" interaction also increases with f, but attains its maximum value at the intermediate values of p (Fig. 4(b)).

4. Discussion

The effects of competitive ability and stress tolerance on the outcome of biotic interactions have been evaluated by a series of field studies (Bertness et al., 1992; Hacker and Bertness, 1999; Choler et al., 2001; Greiner La Peyre et al., 2001; Crain et al., 2004; Liancourt et al., 2005; Wang et al., 2008). However, most of these studies have not considered the long-term dynamics of populations and communities. Here, we used an individual-based model involving two species to theoretically explore this issue further.

4.1. Virtues of our model

The foundation of the model introduced here is the well-known triangular model of primary plant strategies ("CSR") developed by Grime (1973). In our model, both species compete for the cells on the common lattice, and the competitor may exclude the stress-tolerant species through competitive displacement. However, the reverse exclusion cannot happen. At the same time, the stress-tolerant species has a higher fecundity compared to the competitor in harsh environments, providing it with the ability to occupy more empty cells under these conditions. Therefore, the model incorporates a clear trade-off between competitive ability and stress tolerance. Facilitation acts when neighboring species ameliorate the stress experienced by the focal species and increase its fecundity, and the magnitude of this effect increases with the environmental severity gradient studied. Therefore, the variations in competitive and facilitative hierarchies of species along such gradient will be represented in our model more realistically than in dual-lattice models (Travis et al., 2005, 2006; Brooker et al., 2006). This feature makes the model introduced a powerful and efficient tool to investigate the interplay of facilitative and competitive interactions along environmental severity gradients.

4.2. Influence of species strategies on the interplay between facilitation and competition along environmental severity gradients

The joint consideration of the trade-off between competitive ability and stress tolerance had a considerable impact on the outcome of the interaction studied. When the two species were identical with each other, their population dynamics were dominated by the stochastic process of random drift. Facilitation allowed them to persist under high environmental severity conditions, expanding their realized niche (Hacker and Bertness, 1999; Bruno et al., 2003). In the presence of such trade-off, but without facilitation, the realized niche occupied by the stress-tolerant, as well as its density, is reduced to a greater extent than those of the competitor, but both species coexist at intermediate
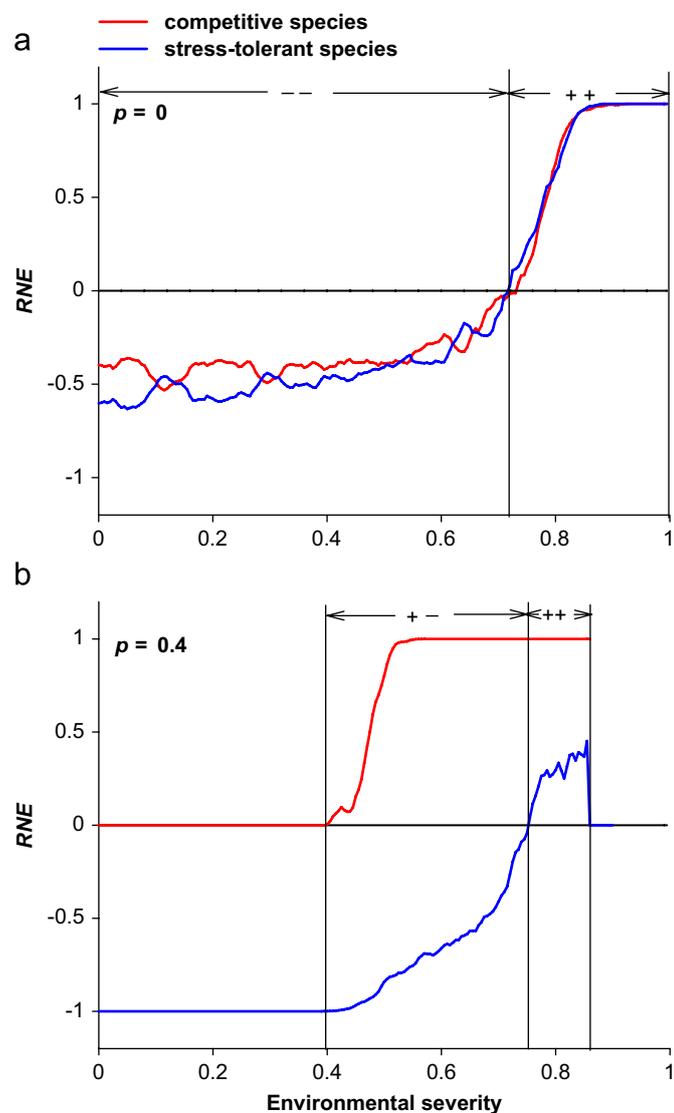

Fig. 3. Relative neighbor effect (*RNE*) index curves summarizing the net outcome of the interaction along the environmental severity gradient when p is either 0 (a) or 0.4 (b). Blue and red lines indicate the *RNE* value of stress-tolerant and competitive species, respectively. "–, –"indicates competitive interactions, "+, –" indicates positive effects for a species and negative for the other, and "+, +" indicates mutualistic interactions. The two species are identical with each other when $p = 0$. The parameter values used in the simulations were the same as those used in Fig. 1. (For interpretation of the references in to colour in the figure legend, the reader is referred to the web version of this article.)
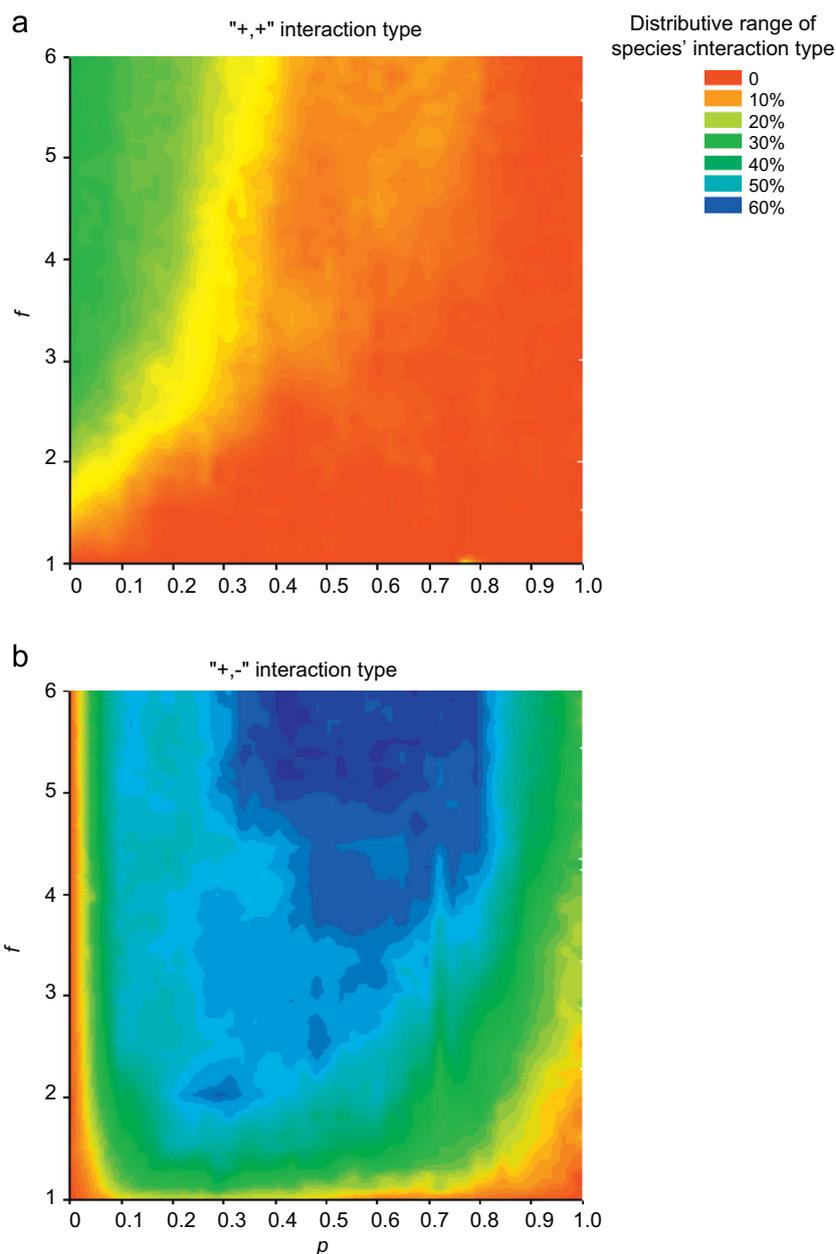
Fig. 4. Variations of the distributive range of species' interaction types with different f and p. (a) "+, +" interaction type, and (b) "+, −" interaction type. The distributive range is calculated as the ratio of the width of distributive range of species' interaction types along environmental severity gradients to the width of total range of environmental severity gradients. p is in the interval $[0, 1)$, sampled in steps of 0.02, and f is in the interval $[1, 6]$, sampled in steps of 0.1. Red region indicates that there is no "+, +" or "+, −" interaction type between species. With the increasing of distributive range of these interactions, their corresponding color will change from red to blue gradually. Other parameter values employed in the simulations are the same as those used in Fig. 1. (For interpretation of the references in to colour in the figure legend, the reader is referred to the web version of this article.)

levels of environmental severity (Fig. 2(g)). These results are in concert with the humped-back models of species richness along environmental stress gradients (Grime, 1973; Michalet et al., 2006). When facilitation is taken into account, there is a large expansion of the realized niche occupied by the competitor, as well as of its coexisting range with the stress-tolerant (Fig. 2(h)), indicating that facilitation is expanding its realized niche. Within its coexisting range with the competitor, facilitation only increases the density of the stress-tolerant in a narrow range at the harshest part of the environmental severity gradient evaluated. Over their coexisting range, the density of the stress-tolerant decreases substantially because its positive effects on the competitor will increase the fitness of the latter and cause the invasion of its own territory.

In our model, despite both species having the same ability to ameliorate environmental harshness (i.e. the facilitation coefficient is the same for both of them), the actual positive effect that a species receives from the other is totally different. This is mainly due to the importance that environmental severity has for the success of the interacting species. The competitor is more susceptible to the environment harshness than the stress-tolerant and thus environmental factors are more important for its success than for that of the latter. In contrast, the stress-tolerant is more susceptible to biotic factors such as competition. Therefore, facilitation benefits more the competitive than the stress-tolerant species, and this benefit will become more intense with the increase in environmental severity. Our modeling results agree with those from field studies suggesting that competitive species

would benefit the most from facilitation. In subalpine and alpine communities of the French Alps (from 2100 m to 2900 m a.s.l.), Choler et al. (2001) found competitive responses for stress-tolerant species and facilitative responses for stress-intolerant species. At lower elevations in the same area (over 700 m a.s.l.), Liancourt et al. (2005) quantified biotic interactions under two water availability levels for three dominant species of contrasted strategies. These authors found that the species with the least tolerance to abiotic stress and highest competitive-response ability was also the most facilitated by neighbors.

4.3. Dynamics of the net outcome of the interaction along environmental severity gradients

When both species are identical with each other, the RNE curves indicate that the net outcome of the interaction will change from competition to facilitation with the increase of environmental severity. This supports the stress gradient hypothesis (Bertness and Callaway, 1994), which predicts that facilitation is more common in conditions of high abiotic stress than when the abiotic environment is relatively benign. When there is a trade-off between species, the RNE curves of competitor and stress-tolerant in our models resemble those proposed by Michalet et al. (2006), which predict that the competitor is more facilitated than the stress-tolerant, and that facilitation peaks first for the competitive species under conditions of intermediate environmental severity. With decreasing environmental severity from the intermediate position along the gradient, the stress-tolerant species is excluded by the competitive, and the importance of facilitation decreases for the competitive species. In the most severe environmental conditions, only the stress-tolerant species can persist because biotic interactions become unimportant relative to the effect of the environment (Michalet et al., 2006).

4.4. Relationships between mutualism and facilitation

When the trade-offs between competitive ability and stress tolerance are considered, the inhabited and facilitated range for the competitor and stress-tolerant species along the environment severity gradient are different from each other, and their facilitated range only overlaps in a very limited zone at the right ends of their coexisting range (Fig. 3). Therefore, mutualistic ("+, +") interactions are limited to the harshest end of their coexisting range, and most of their coexisting range is dominated by "+, −" interactions (Fig. 4). These results agree with a large number of empirical studies suggesting that facilitation mostly occurs as a positive effect of one species on another, with a reciprocal competitive effect from the species receiving the benefits on its benefactor ("+, −" interaction; Callaway, 2007; Brooker et al., 2008). The assumption of dual-lattice models that mutualism is equivalent to facilitation reduces the range of situations over which facilitation can be found in natural communities, and may result in the inaccurate prediction of the impacts of facilitation on the outcome of biotic interactions along environmental severity gradients.

4.5. Limitations of our approach and future developments

Our approach opens an avenue for the inclusion of species strategies into models aiming to explore changes in the interplay between competition and facilitation along environmental severity gradients. However, it has some limitations that need to be acknowledged. First, the dispersal and interaction for both species are constrained to its nearest neighbors in our models. More realistic situations could be achieved by including the dispersal

kernel of the interacting species (Brooker et al., 2008), as well as interaction kernels (Murrell and Law, 2003). Second, when abiotic stress is induced by precisely the same resource needed by the interacting species, such as water in arid and semi-arid environments, facilitation may only occur when neighbors increase its availability (Maestre and Cortina, 2004), something not considered in our model. This effect can be considered in further versions of the model by including competition for this resource when the availability of the resource is lower than a given threshold level (Maestre et al., 2005). Our model could also readily be extended to investigate interactions in multi-species assemblages (Weigelt et al., 2007). This would allow to study how the direct and interactions among multiple species impact the structure of communities along environmental gradients, a crucial issue to understand the consequences of the ongoing climatic change for ecosystem structure and functioning (Brooker, 2006).

5. Conclusion

Our results indicate that the strategies of the interacting species greatly impact the interplay between competition and facilitation along environmental severity gradients, that most of the coexisting range of the interacting species is dominated by "+, −" interactions, and that such range is mainly determined by the trade-off between competitive ability and stress tolerance. They contribute to improve our understanding of the role of positive and negative interactions as a structuring force of natural communities, and of the consequences that changes in these interactions across environmental gradients have for the spatio-temporal dynamics of populations.

Acknowledgments

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