

Threshold facilitations of interacting species

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Abstract The dynamics of species interactions are of central importance for the understanding of ecological coexistence, community structure and the effects of biological invasions. Using bark beetles that colonize the same habitat as an example, we explore species interactions in a resource-based model system with positive feedback between insect abundance and resource availability. The net interspecies interaction was found to be highly dynamic and may alternate in time between competition and mutualism. When both bark beetle species were able to kill trees (“aggressive”), our simulations showed strong facilitations between beetle species. This may lead to escape from control by competition, and increase the frequency of outbreaks of tree-killing. The frequency of net positive interactions varied with interaction strengths and the relative aggressiveness of the species and was highest when both species were strongly aggressive; which predicts disastrous outbreaks if, e.g., the European spruce bark beetle *Ips typographus* and the North American spruce beetle *Dendroctonus rufipennis* should become interacting

species due to introductions. In imbalanced pairs, the relatively less aggressive species was facilitated more often than the aggressive species. Net positive interactions did not occur for strongly inferior species, but their survival was an increasing function of interaction strength with aggressive species and availability of resources. The benefits for the inferior species in the model are consistent with the structure of one aggressive and several less aggressive or non-aggressive species, which is common in bark beetle communities in many parts of the world.

Keywords Bark beetle · Biological invasion · Community structure · Conditional interaction · Mutualism · Niche overlap

Introduction

The niche is one of the fundamental concepts in ecology (Elton 1927). According to the original niche concept, niche differences enable species to coexist in communities and are the basis for the evolution of species diversity (Hutchinson 1957). The concept simply states that, if two species are limited by the availability of the same single resource at the same time and place in a stable community, one of these species will dominate and the other will eventually become extinct (Gause 1934). Interspecific interactions are traditionally described according to their outcome (positive, negative or neutral) for each interacting species (Odum 1971); mutualism (+ +), predation/parasitism (+ −), commensalism (+ 0), and competition (− −). More recent studies suggest that a typological classification of species interactions may be insufficient (Thompson 1988; Bronstein 1994a; Chesson 2000; Wilson and Lundberg 2006) because species interactions may vary due to variation in

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expressions of traits in individuals and population structure. The outcomes may also vary due to variations in insect size, age, life stages, density, or geographic variation in environments in which the species pair is occurring (Thompson 1988; Bronstein 1994a, b; Thompson and Cunningham 2002; Ness et al. 2004).

The dynamics of species interactions is important in many fields of biology, as for example in invasive biology where new interactions are frequent. Still, few studies have explored systems of species interactions that have an intrinsic fluctuation between positive and negative interactions. Here, we consider interspecific interactions that may vary temporally even without taking into account changes in life stage or population structure. Using bark beetles as an example, we show that species in resource-dependent systems may experience net interactions that fluctuate between negative and positive values through time. Specifically, the niche overlap due to feeding and reproducing in the same phloem resource may both reduce reproductive success through resource limitation and facilitate reproduction by combined contribution to tree-killing, which is a positive function of attack density. One species is often inferior (less abundant or successful) compared to the other interacting species (Lawton and Hassell 1981; Kaplan and Denno 2007). There are many possible reasons for inferiority of bark beetles, e.g., lower productivity, lower aggressiveness, or asymmetric interactions in the case of species with similar productivity, aggressiveness, etc. Here, we explore how the frequency of net positive interactions (facilitations), and the survival of strongly inferior species, are related to interaction strength and key characters of the species and the environment, such as the ability to kill and reproduce in trees, the occurrences of storm windfelling, and the availability of trees susceptible to attack in the case of bark beetles. Finally, we compare our model results to niche overlap values occurring in empirical studies of facultative tree-killing bark beetles.

Materials and methods

Bark beetle interactions as a model system

Ips typographus (L.) (European spruce bark beetle) and co-occurring bark beetle species attacking Norway spruce (*Picea abies*) in Scandinavia provide a useful model system for the present model analyses and simulations of how species interactions are affected by thresholded, resource-driven dynamics. Time series analyses of this species have shown a dominance of resource-based dynamics (Økland and Bjørnstad 2003; Økland and Berryman 2004), and competition for breeding substrates and threshold dynamics

seems to be important for regulating populations of many bark beetle species (Berryman and Pienaar 1973; Berryman 1982; Raffa and Berryman 1983).

Bark beetle niches overlap when sympatric bark beetle species can feed on the same phloem resource; i.e., in overlapping regions of the same tree species. Several empirical studies show that the degree of overlap in resource use varies among the bark beetles species that coexist within the same host trees, and that their niches may shift in the presence of interacting species (Paine et al. 1981; Denno et al. 1995; Ayres et al. 2001), and are influenced by interspecific pheromone communication (Byers 2004). Even though aggregation pheromones are mainly effective within a species, more general attractants (e.g., kairomones), such as host terpenes and alcohols, may play important roles in attracting individuals of other species to the same trees (Bakke and Kvamme 1993; Erbilgin et al. 2003, 2007). In addition, there may be cross-attraction due to ubiquitous pheromone compounds, such as ipsdienol (Raffa 2001). For some bark beetle species, it has been found that pheromone communication can have both positive and negative effects on the interaction strengths, and that the pheromone effects may vary between individuals and over time (Birch et al. 1980; Light et al. 1983; Byers et al. 1984; Schlyter and Birgersson 1989; Smith et al. 1990; Borden et al. 1992; Schlyter et al. 1992).

Bark beetle species also differ in dominance and aggressiveness (tendency to attack and kill living trees). Among bark beetles in Northern European forests, *I. typographus* is by far the most numerous, widespread and superior species in outbreaks. This species is one of the most serious pests of spruce in Eurasia, and periodic outbreaks over the past two centuries have caused enormous timber loss in Central and Northern Europe (Grégoire and Evans 2004). Some co-occurring bark beetles on spruce in Europe, such as *Ips duplicatus* Sahlb. (the double-spined bark beetle), *Pityogenes chalcographus* L. (the six-spined spruce bark beetle), *Polygraphus poligraphus* L. (small spruce bark beetle) and *Ips amitinus* Eichh. (the smaller eight-toothed spruce bark beetle) can kill trees or contribute to killing trees; however, they are not so widely distributed, and their outbreaks are infrequent and modest compared to *I. typographus* (Lekander et al. 1977; Grégoire and Evans 2004; Hedgren 2004).

A resource-based Gompertz model has already been formulated for *I. typographus* and has been analyzed with particular reference to the population dynamics of *I. typographus* in Scandinavia, for which a comprehensive literature allows full parameterization (Økland and Bjørnstad 2006). The model reproduces the general behavior of the bark beetle outbreak dynamics reasonably well, and the results are consistent with historical outbreak periods. The basic model is

$$N_t = N_{t-1} \exp \left[a \left(1 - \frac{\log N_{t-1}}{\log K_t} \right) \right], \tag{1}$$

where N_t is the population density in year t , a is the Gompertz growth rate, and K_t is the resource base (often denoted “carrying capacity”) (Økland and Bjørnstad 2006).

A key property of this model is the existence of a population threshold for resource availability that causes a variant of the Allee effect. The resource consists of two components: wind-felled trees and living trees that are susceptible to beetle attacks. The first is available in highly variable amounts drawn from an empirical frequency of large windfall episodes (Økland and Bjørnstad 2006). The latter resource is only available when the beetles are sufficiently abundant to colonize living trees, i.e., above the abundance threshold L , which may vary with the level of drought stress of the host trees. The resource base in the one-species threshold system (Eq. 1) is thus given by

$$K_{w,t} = b_w(W_0 + W_t), \quad \text{if } N \leq L, \tag{2a}$$

$$\begin{aligned} K_{w+s,t} &= K_{w,t} + K_{s,t} \\ &= b_w(W_0 + W_t) + b_s(S_{acc} + S_{add} - A_t), \\ &\quad \text{if } N > L, \end{aligned} \tag{2b}$$

where $K_{w,t}$ is a function of the volume of wind-felled spruce trees (background windfelling W_0 plus occasional storm windfelling W_t) and the number of beetles produced per m^3 of wind-felled trees (b_w), and $K_{s,t}$ is a function of the accumulated volume of standing susceptible trees (S_{acc}), the volume of susceptible trees added each year (S_{add}), the annual consumption of standing resources by the bark beetles (A_t ; proportional to beetle abundance) and the number of bark beetles produced per m^3 of standing susceptible trees (b_s) (Økland and Bjørnstad 2006).

In the present study, the model was extended to include more than one species that use the same resources. Following Lotka (1925) and Volterra (1926), the competition coefficients α_{ij} express the influence of one species’ abundance upon the other, and can be interpreted as a quantification of the general interspecific interaction strength (Lotka 1925; Volterra 1926) without describing in detail the biological mechanisms that are involved for individual species (Paine et al. 1981; de Jong and Sabelis 1988; Flamm et al. 1989; Rankin and Borden 1991; Schlyter and Anderbrant 1993). By extending the basic Gompertz model (Eq. 1) with one species, we thus obtain a two-species interaction model:

$$N_{i,t} = N_{i,t-1} \exp \left[a \left(1 - \frac{\log [N_{i,t-1} + \alpha_{ij} N_{j,t-1}]}{\log K_{i,t}} \right) \right], \tag{3}$$

where the subscripts i and j denote species i and j , respectively. Here, it is assumed that $K_i = K_j = K$.

In the Lotka–Volterra model of competition, an increasing abundance of a competitor will generally result in an inhibitory effect. The outcome is more complex in the interaction model considered here (Eq. 3), as increasing abundance of a second bark beetle species (and their fungal associates; Franceschi et al. 2005) may be beneficial when it contributes to surpassing the threshold for colonizing living trees, and thereby achieving a positive feedback by creating more habitat, but otherwise the effect is inhibitory through a combined exhaustion of the resource base (Økland and Bjørnstad 2006). This general interaction model applies to many facultative tree-killing bark beetles, even though individual species of bark beetles may require modifications to include mechanisms in other systems and regions, such as predator swamping (Ayres et al. 2001; Aukema and Raffa 2004), or interaction dynamics with fungal and mite associates (Hofstetter et al. 2006).

Our basic questions related to the balance between the species was how and under what circumstances each species increases or decreases in abundance in response to the abundance of the other species, and how the frequency of net positive interactions and the survival of inferior competitors are related to interaction strengths and aggressiveness of the species. The general dynamics of the interaction model were studied by isocline analyses, and the frequencies of net positive interactions and survival were explored in simulations. Finally, we compared the model results to niche overlap values occurring in empirical studies of facultative tree-killing bark beetles in general, and especially for facultative tree-killing bark beetles that interact with *I. typographus*. All empirical values were based on Levins’ formula of niche overlap (Levins 1968; Colwell and Futuyma 1971) ranging from 0 to 1. The empirical values were found in or calculated from data in previous publications (Ringsgård 1975; Paine et al. 1981; Zumr 1984; Grünwald 1986; Amezega and Rodríguez 1998; Jakus 1998).

Model analyses and simulations

A measure of the balance between positive and negative net effects of the interaction was developed to quantify the reciprocal interaction effect. For each annual step, the abundance of each species was modeled both with and without an effect of interaction with the other species. $N_{i,t}$ denoted the abundance in year t of species i with no interaction effect (i.e., with only species i present), and $N_{i,j,t}$ denoted the abundance of species i with an interaction effect of species j (both species present). The interaction effect of species j on species i ($\Delta R_{i,j,t}$) was defined as the difference between the net per capita growth rate (e.g., Case 2000) with an interaction effect

($R_{i,j,t} = N_{i,j,t}/N_{i,j,t-1} - 1$) and the growth rate without an interaction effect ($R_{i,t} = N_{i,t}/N_{i,t-1} - 1$):

$$\Delta R_{i,j,t} = R_{i,j,t} - R_{i,t} = \frac{N_{i,j,t} - N_{i,t}}{N_{i,j,t-1}}. \quad (4)$$

Plotting $\Delta R_{i,j}$ against time was used to demonstrate the typical fluctuation between net positive and negative interactions for two species with slight differences in competition coefficients and similar aggressiveness (net positive interactions do not occur for species with pronounced differences in relative aggressiveness and competition coefficients; see below). Isocline analyses were applied to detect the underlying dynamics in the model of populations with fluctuating interactions.

The dynamics of the model was explored by varying the aggressiveness and the interaction strengths of the species within an environmental regime corresponding to that of *Ips typographus* in Scandinavia (i.e., with univoltinism and empirical windfelling distribution) (Økland and Bjørnstad 2006). The frequency of years with a positive effect of the presence of a second species (Fig. 3) and the survival of a strongly inferior species (Fig. 4) were quantified in ten simulated time series at each set of (16×16) parameter values. The trends of the relationships were emphasized by averaging over the repeated simulations at each set of parameter values before presentation in surface plots. The relative aggressiveness of each species (d_i) was entered into the model as coefficients weighting the contribution of each species in the criterion for surpassing the threshold density of beetles needed to kill living trees (L) in each time step t :

$$\sum_i d_i N_{t,i} > L \quad (5)$$

Studying the frequency of net positive interactions (Fig. 3), one of the species was kept at maximum aggressiveness ($d_1 = 1$) in all simulations, which could be a realistic scale level for the most aggressive species (e.g., *I. typographus* in Eurasia and *Dendroctonus ponderosae* in North America) relative to their interacting species. Since bark beetle species that are interacting with *I. typographus* vary in their ability to kill trees, a range of d values (1, 1/2, 1/8) was used in the model simulations. In the study of survival (Fig. 4), the strongly inferior species was given a lower aggressiveness ($d_2 = 1/8$) and production of beetles per colonized trees ($b_{a,2} = 100$ beetles/m³) relative to the first species ($d_1 = 1$, $b_{a,1} = 200$ beetles/m³). Beetle densities per volume were based on estimates from Scandinavian spruce systems used in the resource-depletion model (Økland and Bjørnstad 2006). All simulations were performed within wide ranges of competition coefficients ($\alpha_{1,2}$ and $\alpha_{2,1}$ varying from 0.1 to 2.0 in Fig. 3, and $\alpha_{2,1}$ varying from 0.1 to 1.5 in Fig. 4). The average population survival

time (years) for the inferior species was studied while varying the interaction strength of the inferior species on the superior species ($\alpha_{2,1}$) and two environmental variables: the yearly probability of a big windfall event (p_w , Fig. 4a) and the volume (m³) of susceptible trees added per km² every year (S_{add} , Fig. 4b). The interaction strength of the superior species on the inferior species ($\alpha_{1,2}$) was kept high (1.5) in all of the survival simulations.

Results

The net interaction effect ($\Delta R_{i,j,t}$) is negative most of the time for both species (Fig. 1); however, spikes of net positive interactions occur at irregular intervals when the total abundance of beetles ($\Sigma N = N_i + N_j$) is close to the threshold L . These short periods of net positive

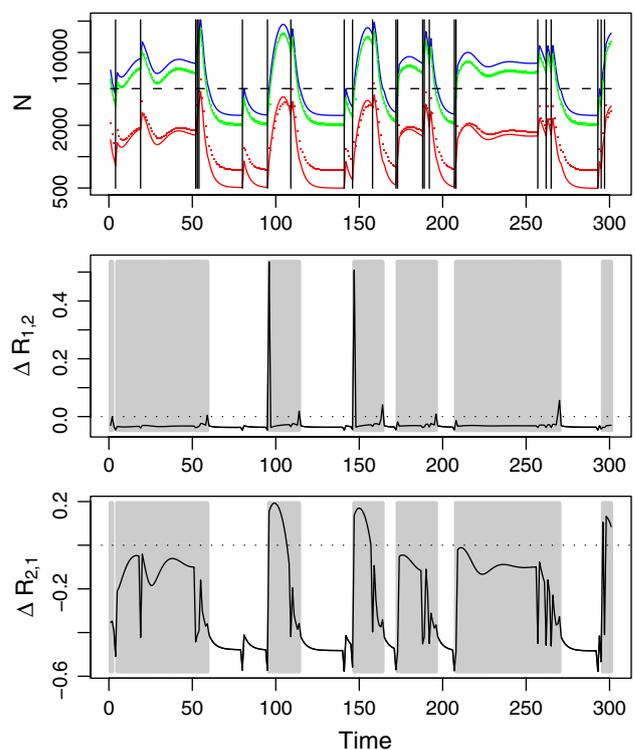


Fig. 1 Typical example of simulated time series for two interacting bark beetles with fluctuating interactions. *Upper panel*: No. of beetles (N) of species 1 (superior, green), species 2 (inferior, red) and the summed abundance (blue) plotted against time (no. of years). *Solid lines* indicate abundances with interaction and *dotted lines* indicate abundances in the absence of interaction. The colonization threshold (L) is indicated by a dashed line; windfall events are indicated by *black vertical lines*. *Lower panels*: time series of interaction effects ($\Delta R_{i,j}$, see explanation in “Materials and methods” section). *Gray shading* indicate periods when the beetles are sufficiently abundant to colonize susceptible living trees ($\Sigma N > L$). Aggressiveness is assumed to be similar ($d_1 = d_2 = 1$), and competition coefficients are slightly different ($\alpha_{1,2} = 0.9$, $\alpha_{2,1} = 0.6$)

interactions are associated with large perturbations (windfall episodes; vertical lines in upper panel) that cause population increases above L , or with periods where ΣN drops at the end of periods above L . The net interspecific interactions switch between negative and positive both when the rate of perturbations is stochastic and when it is kept constant. After long periods below L , the following periods of $\Delta R > 0$ are usually more positive and long-lasting (middle and lower panels in Fig. 1). The superior species (middle panel) tends to have shorter spikes of net positive interaction, mainly because it will more quickly become independent of the other species to stay above the threshold L . In contrast, the inferior species (lower panel) has longer periods of net positive interactions due to its stronger dependency of the other species for staying above L . The system has two stable equilibria; one below the colonization threshold L (evident in several stable periods below the threshold in Fig. 1), and one above the threshold (most evident in the stable period around $t = 250$; Fig. 1). When the system is undisturbed, it eventually settles at one of the two equilibria, while perturbations (e.g., storm windfelling) or a drop in beetle abundance (e.g., as an effect of resource consumption and resource depletion) may cause shifts between the equilibria, as shown in the following analysis.

In the original one-species Gompertz model (Eq. 1) the equilibrium density where the population density remains constant is $N^* = K$. In the two species model (Eq. 3), assuming that $K_i = K_j = K$, the equilibrium densities are

$$N_i^* + \alpha_{ij}N_j^* = K, \tag{6a}$$

$$N_j^* + \alpha_{ji}N_i^* = K. \tag{6b}$$

Rearranging these equations gives

$$N_i^* = \frac{1 - \alpha_{ij}}{1 - \alpha_{ij}\alpha_{ji}} N_j^*, \tag{7a}$$

$$N_i^* = \frac{1 - \alpha_{ij}}{1 - \alpha_{ij}\alpha_{ji}} K. \tag{7b}$$

Thus, the equilibrium density of species i is proportional (with proportionality constants determined by the competition coefficients) to the equilibrium density of species j , and to the resource base. Fluctuations in the resource base cause shifts between the two equilibria. When the system is below the colonization threshold (i.e., $\Sigma N \leq L$) the resource base is determined by windfelling only (K_w); when the system is above the colonization threshold, the second resource is also available ($K_{w+s} = K_w + K_s$) (Fig. 2). In neither case is K a constant: it is shifted up and down by stochastic storm windfellings and consumption of resources (Eq. 2). However, in the absence of storm windfellings, K approaches a constant value determined by the balance between the addition and consumption of resources. Below the colonization threshold $K = b_w W_0$. Above the colonization threshold, $K = L + S_{\text{add}}/h_s$ (this can be found by noting that $A^* = S_{\text{add}}$ and $A^* = h_s N - h_s L$, where h_s is the slope and $-h_s L$ is the intercept in the linear relation; Økland and Bjørnstad 2006). Thus, in the absence of storm windfellings, the equilibria are

$$N_i^* = \frac{1 - \alpha_{ij}}{1 - \alpha_{ij}\alpha_{ji}} b_w W_0, \quad \text{if } \sum_i d_i N_i \leq L \tag{8a}$$

$$N_i^* = \frac{1 - \alpha_{ij}}{1 - \alpha_{ij}\alpha_{ji}} \left(L + \frac{S_{\text{add}}}{h_s} \right), \quad \text{if } \sum_i d_i N_i > L. \tag{8b}$$

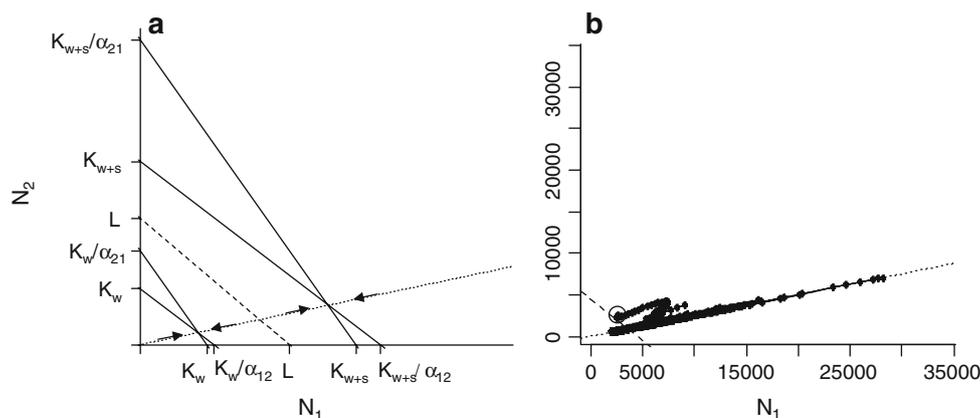


Fig. 2 Isocline plot (a) summarizing the dynamics of the interaction model (Eq. 3). When the system is below the colonization threshold (dashed line) the zero-growth isoclines of the two species (solid lines) define a stable equilibrium determined by the resource base for the primary resource (K_w) and the competition coefficients ($\alpha_{1,2}$ and $\alpha_{2,1}$). When the system is above the colonization threshold, the equilibrium is defined by the sum of both resources (K_{w+s}). In the absence of

external perturbations affecting the species differentially, the system always moves along the equilibrium line (dotted) defined by the competition coefficients (Eq. 8). This is illustrated in the phase plane plot (b) of a time series of the bark beetle system (Eq. 3). The system starts at the open circle and moves in annual steps (filled circles) towards an equilibrium line (dotted), occasionally crossing the colonization threshold ($\Sigma N > L$; dashed)

Storm windfellings cause violent deviations from these equilibria, and often bring the system across the colonization threshold (Fig. 2b). This causes shifts in equilibrium states and fluctuating interactions between the species (Fig. 1). However, the system always moves towards one of the equilibrium states where the ratios of the species abundances are constant, after an initial period of non-equilibrium dynamics (Fig. 2b). This ratio is determined by the competition coefficients (Eq. 7) and remains constant regardless of perturbations such as storm windfelling.

Even when species live side by side without overlapping on the tree ($\alpha_{1,2} = \alpha_{2,1} = 0$), sometimes the same species may have a net positive interaction by enabling the total abundance of beetles to pass the colonization threshold and kill their host (Fig. 3a, b). However, the degree of interaction strength has a marked effect on the frequencies of net positive interactions. Increasing the interaction strength causes a reciprocal effect on the population dynamics of both species, which in turn increases the frequency of years with net positive interaction. For all parameter sets tested, a certain area in the parameter space of interaction strengths ($\alpha_{1,2}$ and $\alpha_{2,1}$) appears as an optimum for the frequency of net positive interactions; however, the size and the position of the optimum within the parameter space of interaction strengths are influenced by the relative aggressiveness of the species (Fig. 3). When both species are highly aggressive ($d_1 = d_2 = 1$; Fig. 3a, b), the maximum frequency of net positive interactions is about the same for both species (63%), and the maxima occur symmetrically for intermediate values of interaction strengths ($\alpha_{1,2} = 0$ and $\alpha_{2,1} = 0.45$ for species 1, and $\alpha_{1,2} = 0.45$ and $\alpha_{2,1} = 0$ for species 2). Decreasing the relative aggressiveness of species 2 results in an increase of frequency of net positive interactions for species 2 down to a relative aggressiveness about $d_2 = 0.5$ (maximal frequency 74.5%), while the maximal frequency of net positive interactions for species 1 is decreasing in the same interval (Fig. 3c, d). Further decrease in d_2 below 0.5 results in a declining maximum of net positive interactions for both species. When the relative aggressiveness of the species 2 is $d_2 = 1/8$, the more aggressive species (species 1) experiences near zero net positive interactions, while the frequency of net positive interactions is still significant for the second species (Fig. 3e, f).

A strongly inferior species on the border to extinction does not contribute significantly to pass the threshold for colonizing living trees. Our simulations show that $\Delta R_{i,j}$ is always negative when the second species is strongly inferior ($d = 1/8$, $b_a = 100$ and $\alpha_{2,1} < \alpha_{1,2}$), implying that occasional facilitations do not occur. In this situation, the interaction strength of the inferior species on the superior species ($\alpha_{2,1}$) is an important factor for chancing

survivorship. In all the simulations (Fig. 4), the mean survival length of the inferior species increases as a function of $\alpha_{2,1}$ in the whole range of values tested (0–1.5) and is also favored by resource availability in most of the parameter space. When $\alpha_{2,1}$ is small, the survival length is a positive function of the resource variables, such as the yearly probability of big windfall event (p_w ; Fig. 4a) and the volume of susceptible trees added every year (S_{add} ; Fig. 4b). At high $\alpha_{2,1}$ -values, such relationships form non-linear functions with minima for intermediate values of p_w and S_{add} (Fig. 4). Increasing the interaction strength with the superior species ($\alpha_{2,1}$) becomes increasingly important for the survival at low resource values, as the survival approaches zero at low values of p_w and $\alpha_{2,1}$ and is dramatically increasing with increasing $\alpha_{2,1}$ (Fig. 4).

Empirical niche overlap values between pairs of bark beetles vary considerably, both among facultative tree-killing species and among other species (Table 1). With a few exceptions, the pairs of values are imbalanced, favoring one species over the other. Many species interacting with *I. typographus* show fairly high niche overlap values. Different records of the same species pairs show quite different niche overlap values, indicating highly dynamic interactions in space and time.

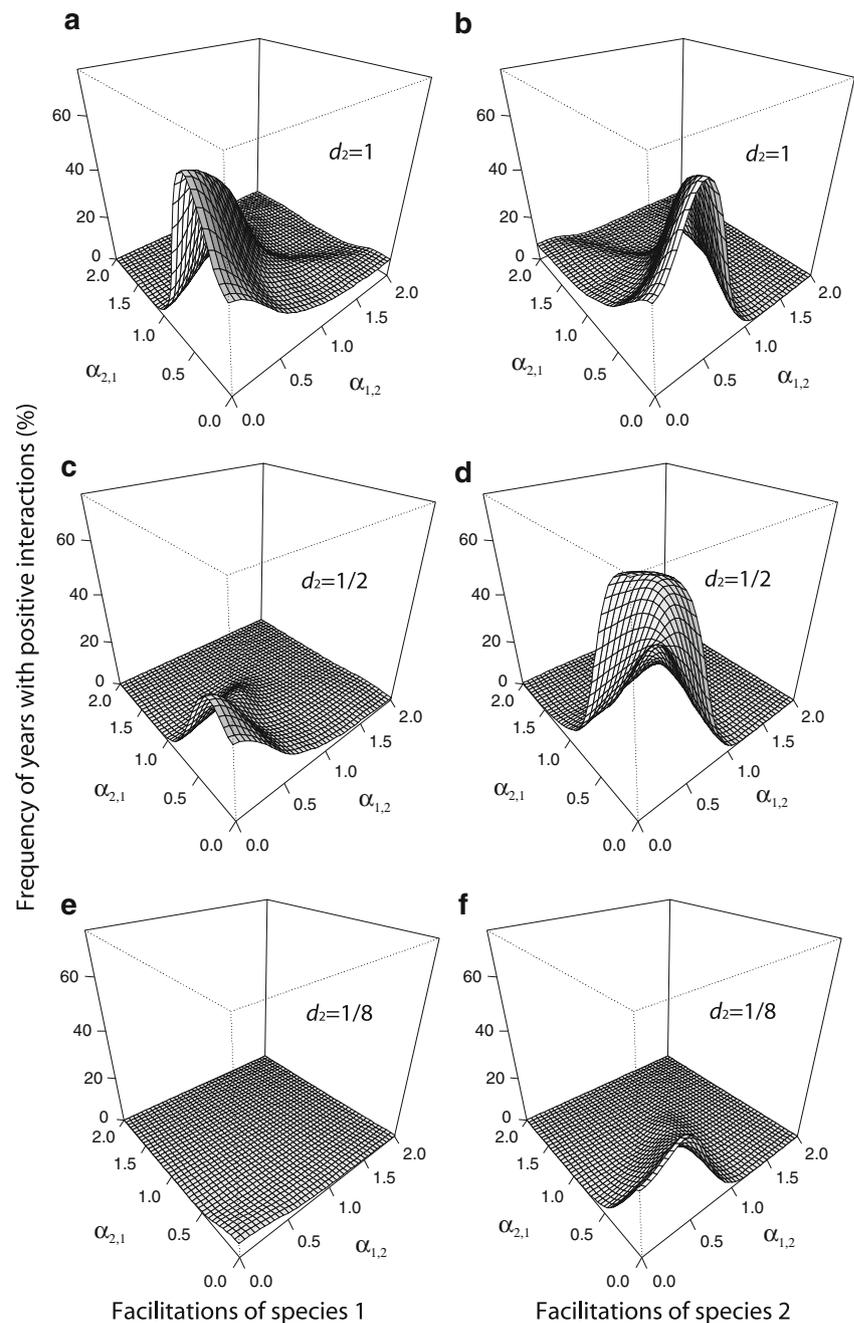
Discussion

Interspecific interactions between species that are heavily dependent on the same limited resources are often negative. Still, many species maintain a high degree of niche overlap, despite competition for a resource, when the benefit of access is greater than the cost of competition. For bark beetles, maximizing access to phloem resources is probably the main reason why so many species have (at least partially) overlapping ranges within their host tree.

In the model presented, the net result even of competitive interactions can be positive, depending on population state. At certain levels of competitive interactions ($\alpha_{1,2}$ and $\alpha_{2,1}$), the competition cost may be modified by sporadic facilitations (mutualisms) that enables both species to access additional resources (living trees). The outcome of competition and facilitations in the model is highly dynamic, which is consistent with the large variation in empirical niche overlaps among bark beetles, even within the same species pairs (Table 1). According to the isocline analysis, the occurrence of facilitations is strongly dependent on density thresholds for colonization and the development of resource availability and population sizes.

As facilitation may alter many basic predictions (competitive exclusion, etc.), it is argued that facilitation should more often be included into the theory, models and paradigms of population and community ecology (Stachowicz

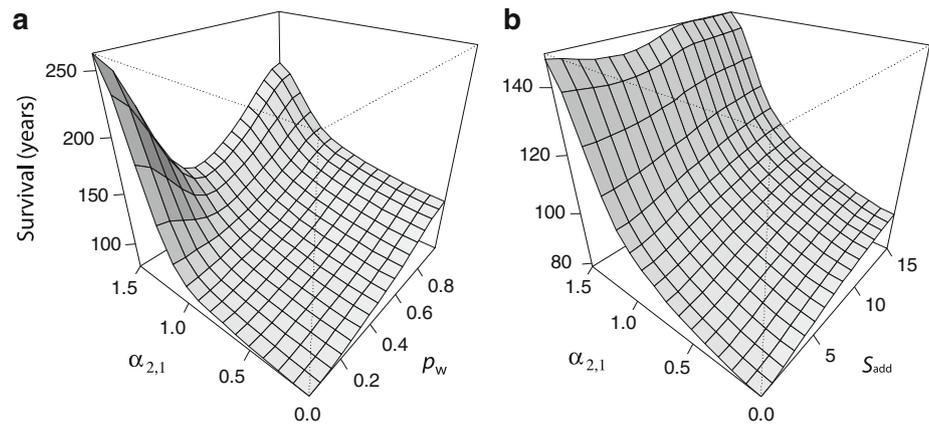
Fig. 3 The frequency of years with net positive interactions for species 1 (**a, c, e**) and species 2 (**b, d, f**) when varying the coefficients of interaction strengths ($\alpha_{2,1}$ and $\alpha_{1,2}$) and the aggressiveness of the species (d). The interaction of species 1 on 2 ($\alpha_{1,2}$) and the interaction of species 2 on 1 ($\alpha_{2,1}$) were varied from 0.1 to 2.0. The relative aggressiveness of species 1 was kept at maximum value ($d = 1$) in all simulations, while the relative aggressiveness of species 2 was varied ($d = 1$ for a strong competitor in **a** and **b**, $d = 1/2$ for a medium competitor in **c** and **d** and $d = 1/8$ for a weak competitor in **e** and **f**)



2001; Bruno et al. 2003; Kaplan and Denno 2007). For bark beetles, the ability to get released from competitors and natural enemies is assumed to be an essential component of why aggressive species can become epidemic, and several mechanisms have been proposed for avoidance of competition and predators (Schlyter and Anderbrant 1993; Savoie et al. 1998; Ayres et al. 2001; Raffa 2001; Byers 2004; Campbell and Borden 2006; Schroeder 2007; Raffa et al. 2008). According to our simulation results, the degree of facilitations between species varies with the relative aggressiveness of species and the strength of interaction

between species involved. For species pairs with little or moderate differences in aggressiveness, niche differentiation is often not beneficial, as the frequency of facilitations may be high when niches overlap (Fig. 3). In contrast, if differences in aggressiveness between species are high (i.e., one is more aggressive than the other), then our model predicted only sporadic facilitations between species. For example, most bark beetles that co-occur with *I. typographus* on Norway spruce in Scandinavia are much less aggressive than *I. typographus*, suggesting only sporadic facilitations in the proposed model system. However,

Fig. 4 The mean survival time of a strongly inferior species as a function of interaction strength of the inferior species on the superior species ($\alpha_{2,1}$) and **a** the yearly probability of big windfall event (p_w), or **b** the volume (m^3) of susceptible trees added per km^2 every year (S_{add})



introduction of a highly aggressive bark beetle species, e.g., the North American spruce beetle, *Dendroctonus rufipennis*, could potentially result in higher frequency of severe outbreaks due to strong facilitations between *I. typographus* and *D. rufipennis*. Considering economic damage caused by either species in their respective regions (Christiansen and Bakke 1988; Wood and Van Sickle 1992), interactive dynamics that facilitates both species in the same area could be disastrous.

The fluctuations between negative and positive net interspecific interactions in the proposed model is intrinsic to the population dynamics, and is not a direct result of mechanisms related to the age, size or life span of individuals, to demographic or genetic structure, or to geographical variation in environmental factors (Wolin and Lawlor 1984; Thompson 1988; Bronstein 1994b; Holland et al. 2002; Thompson and Cunningham 2002). However, the environmental factors may indirectly influence the rate of net positive or negative interactions, and may even stop the fluctuations when the populations are limited from surpassing the threshold for colonizing living trees. Both the frequency of large windfall events and the rate of resource accumulation (living trees that are susceptible to beetle attacks) are important factors determining the periodicity of net positive interactions, and also for the survival of strongly inferior species, for which facilitations do not occur (Fig. 4). Judged from the high frequency of large storms (1 every 11 years during the last 50 years in Scandinavia; Benestad 2005), the fluctuations of interactions should be sufficiently high for having a significant influence on the population dynamics of interacting bark beetles. The frequency of periods above the density threshold of colonizing living trees is also a function of the accumulation rate of susceptible trees (Appendix B in Økland and Bjørnstad 2006), which is a factor that varies significantly between forest landscapes and may have been much higher in the ancient forest landscapes before the

influence of human beings on forest structure (Siitonen 2001). Resource-dependent interactions have also been recognized in other systems, such as parasitic trematodes and helminths (Thomas et al. 1997), and measles and whooping cough (Rohani et al. 2003).

The inferior species appear to benefit most from the interaction, which agrees well with the long tail of inferior or secondary species occurring together with *I. typographus* (Lekander et al. 1977). For low or moderate differences in aggressiveness (d) and beetle production (b_a), the frequency of facilitations for the inferior species is significantly larger than for the superior species (Fig. 3d, f). Correspondingly, experimental studies of the inferior species *Pityogenes chalcographus* showed a significantly higher success in trees also inhabited by *I. typographus* (Hedgren 2004). Facilitations due to competitive interactions do not occur if the second species is strongly inferior because of low aggressiveness (d_2) or beetle production ($b_{a,2}$). Even without facilitations, the inferior species increases its survival by increasing its interactive influence on the superior species ($\alpha_{2,1}$; see Fig. 4). This is consistent with large number of co-occurring bark beetles that show a considerable niche overlap with *I. typographus* on spruce (Table 1). According to Lekander et al. (1977), 23 species with spruce as a principal host are sympatric with *I. typographus* in Scandinavia. All of these species are much less aggressive than *I. typographus* and are strongly inferior all the time, or some of these species may occasionally contribute to tree-killing (e.g., *P. chalcographus*, *Polygraphus poligraphus*, *I. duplicatus*). Empirical studies show that these species overlap with *I. typographus* in the same habitat during and after bark beetle outbreaks (Lekander et al. 1977; Grodzki et al. 2004), and their niche overlaps with *I. typographus* are fairly high (Table 1).

Facilitations may play an important role for the structure of bark beetle communities. When resources are available, the frequency of facilitations from interacting

Table 1 Empirical niche overlap values between different pairs of bark beetles associated with Norway spruce or other conifer species

Species pairs	Niche overlap	Source
Facultative tree-killing bark beetles on Norway spruce		
<i>Ips amitinus</i> – <i>Ips typographus</i>	0.62–0.60	Zumr (1984)
<i>Ips amitinus</i> – <i>Pityogenes chalcographus</i>	0.92–0.63	Zumr (1984)
<i>Ips typographus</i> – <i>Ips duplicatus</i>	0.19–0.10	Ringsgård (1975)
<i>Ips typographus</i> – <i>Pityogenes chalcographus</i>	0.31–0.22	Zumr (1984)
<i>Pityogenes chalcographus</i> – <i>Ips typographus</i>	0.92–0.90	Ringsgård (1975)
<i>Pityogenes chalcographus</i> – <i>Ips typographus</i>	0.81–0.68	Grünwald (1986)
<i>Pityogenes chalcographus</i> – <i>Ips duplicatus</i>	0.29–0.16	Ringsgård (1975)
Other bark beetles on Norway spruce		
<i>Hylurgops palliatus</i> – <i>Xylechinus pilosus</i>	0.04	Jakus (1998)
<i>Xylechinus pilosus</i> – <i>Hylurgops palliatus</i>	0.02	Jakus (1998)
<i>Hylurgops palliatus</i> – <i>Xyloterus lineatus</i>	0.85	Jakus (1998)
<i>Xyloterus lineatus</i> – <i>Hylurgops palliatus</i>	0.63	Jakus (1998)
<i>Xylechinus pilosus</i> – <i>Xyloterus lineatus</i>	0.00–0.00	Jakus (1998)
<i>Xyloterus lineatus</i> – <i>Xylechinus pilosus</i>	0.00–0.00	Jakus (1998)
Facultative tree-killing bark beetles on pines		
<i>Dendroctonus frontalis</i> – <i>Ips grandicollis</i>	0.06–0.02	Paine et al. (1981)
<i>Ips avulsus</i> – <i>Dendroctonus frontalis</i>	0.14–0.08	Paine et al. (1981)
<i>Ips avulsus</i> – <i>Ips calligraphus</i>	0.69–0.45	Paine et al. (1981)
<i>Ips avulsus</i> – <i>Ips grandicollis</i>	0.31–0.08	Paine et al. (1981)
<i>Ips calligraphus</i> – <i>Dendroctonus frontalis</i>	0.34–0.31	Paine et al. (1981)
<i>Ips calligraphus</i> – <i>Ips grandicollis</i>	0.14–0.06	Paine et al. (1981)
Other bark beetles on pines		
<i>Ips sexdentatus</i> – <i>Orthotomicus erosus</i>	1.00–0.40	Amezega and Rodríguez (1998)
<i>Ips sexdentatus</i> – <i>Orthotomicus erosus</i>	0.83–0.36	Amezega and Rodríguez (1998)
<i>Ips sexdentatus</i> – <i>Orthotomicus erosus</i>	0.66–0.51	Amezega and Rodríguez (1998)
<i>Ips sexdentatus</i> – <i>Pityogenes bidentatus</i>	0.61–0.22	Amezega and Rodríguez (1998)
<i>Ips sexdentatus</i> – <i>Tomicus piniperda</i>	0.93–0.77	Amezega and Rodríguez (1998)
<i>Orthotomicus erosus</i> – <i>Pityogenes bidentatus</i>	1.00–0.56	Amezega and Rodríguez (1998)
<i>Tomicus piniperda</i> – <i>Ips sexdentatus</i>	0.84–0.76	Amezega and Rodríguez (1998)
<i>Tomicus piniperda</i> – <i>Ips sexdentatus</i>	0.83–0.68	Amezega and Rodríguez (1998)
<i>Tomicus piniperda</i> – <i>Orthotomicus erosus</i>	0.78–0.31	Amezega and Rodríguez (1998)
<i>Tomicus piniperda</i> – <i>Orthotomicus erosus</i>	0.65–0.31	Amezega and Rodríguez (1998)
<i>Tomicus piniperda</i> – <i>Orthotomicus erosus</i>	0.60–0.38	Amezega and Rodríguez (1998)
<i>Tomicus piniperda</i> – <i>Pityogenes bidentatus</i>	0.50–0.24	Amezega and Rodríguez (1998)
<i>Tomicus piniperda</i> – <i>Pityogenes bidentatus</i>	0.27–0.08	Amezega and Rodríguez (1998)

The values are estimated by Levins formula of niche overlap (Levins 1968), and are presented in descending order within each category of the table

species may be an additional factor for how often aggressive beetles will be released from competitors and become epidemic, which in turn creates more habitat for secondary bark beetle species. It has been recognized that positive interactions can have cascading effects throughout the communities (Stachowicz 2001). The current simulations showed that relatively nonaggressive bark beetles benefit from interaction with the most aggressive bark beetle species, which is a pattern found in bark beetle communities in different regions of the world (Lekander et al. 1977; Berryman 1988; Ayres et al. 2001). As

traditional paradigms of interspecific interactions do not correspond well with published studies of phytophagous insects, Kaplan and Denno (2007) called for a new paradigm that accounts for indirect interactions and facilitation. Threshold facilitations of interacting species, such as the complex interaction of bark beetle systems, should be taken into account in new theory developments. As demonstrated here, the facilitations of such systems may vary in time and depend on resource availability, characters of the interacting species (degree of niche overlap and aggressiveness), and the frequency of outbreaks.

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