Chapter 6

When competition is good for you: Emergent facilitation among competing predators

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Abstract

It has recently been shown that an Allee effect (positive density dependence at low population density) can occur in a population of a predator that is specialized on one stage of the life cycle of its prey, when the prey population is regulated by food- or density-dependent development. Through overcompensation in the prey regulation, feeding by the predator can increase the density of prey in the stage that it feeds on, thereby facilitating its own food source and creating an Allee effect. Alternatively, such a predator may increase the density of prey in other life stages. In this paper, we study the interaction effect of two predators that each feed exclusively on one specific life stage of a shared prey population. We find that a predator feeding on the regulating (immature) prey stage can strongly increase the prey density for a predator feeding on adult prey, leading to greatly increased persistence of the adult predator. The facilitation is not mutual; the predator that feeds on the regulating stage can persist alone, and is always strongly reduced in density by the presence of the adult-specific predator. Our results add a new perspective to the discussion about coexistence of similar competitors. We show that within-species processes such as density dependent development can lead to unexpected and counterintuitive interactions at the community level.
6.1 Introduction

The majority of interactions in ecological communities are of a consumer-resource type, where one (stage of a) population or species feeds on another. The influence of the consuming stage, population or species on its resource is hence inherently negative. Although a number of studies throughout the past decades have stressed that positive interactions (often referred to as facilitation) may be equally important (Addicott, 1984; Boucher, 1985; Bertness and Callaway, 1994), ecological research is still dominated by studies of negative interactions. In a recent review, Bruno et al. (2003) note that the importance of facilitation is slowly being acknowledged. They also show that both direct and indirect positive interactions may strongly affect a wide range of ecological theory.

One notable exception to the research focus on negative interactions concerns the intraspecific positive interaction at low population density coined the Allee effect. A number of mechanisms such as mate search difficulty or inefficacy of social behavior at low population density have been advanced to generate an Allee effect (Courchamp et al., 1999; Stephens and Sutherland, 1999; Boukal and Berec, 2002). This positive density dependence at low density is widely appreciated as an important factor that threatens many endangered species, and can cause an unexpected drastic decline (catastrophic collapse) of a population (Stephens and Sutherland, 1999).

Recently, De Roos and Persson (2002), De Roos et al. (2003b) and VanKooten et al. (2003) (chapter 5 in this thesis) have shown a new mechanism that can lead to the Allee effect, through the interplay of intra-specific competition among and size-selective predation on prey individuals. They show that it can emerge in a predator feeding on a specific stage of its prey, if the inflow into that stage is regulated through scramble competition. Through overcompensation in the regulatory mechanism of the prey population, predators will decrease the density of prey engaged in the scramble competition, but may thereby actually increase the density of vulnerable prey. This autocatalytic effect of predation can lead to increased persistence of the predator, but it also creates a minimum density threshold below which the predator population will go extinct, and increases the risk of a catastrophic collapse of the predator population. Besides the density-increase in the stage that it feeds on, De Roos et al. (2003a) show that a size-specific predator can, through the same mechanism, also increase the density of prey in other stages. For example, a predator feeding on a juvenile prey stage can cause an increase in the adult prey density.

It is this particular trait of the interaction that has led to the central question of this paper: Is it possible that a predator which feeds specifically on one prey stage and thereby causes an increased density in another prey stage, facilitates the persistence of a competing predator feeding specifically on this increased prey stage? In particular, could such facilitation, which emerges from the prey ontogeny and population feedback, increase the persistence range and reduce the risk of a catastrophic collapse in a stage-specific predator population which is exposed to an emergent Allee effect? Throughout the rest of this paper, we use the term emergent
facilitation to indicate this phenomenon; an increased persistence range of one of the predator species as a consequence of the change in prey stage distribution induced by the other predator.

We find that for a broad range of ecological conditions, emergent facilitation occurs. The persistence range of a predator feeding on the adults of a food- or development-regulated prey population is greatly enlarged by the presence of another predator, feeding on juveniles of the same species. In a broad range of parameter values, the adult-specific predator can only occur when the juvenile-specific predator is present to facilitate it, and this effect greatly increases the parameter range under which the facilitated adult-specific predator can persist. The interaction is not mutualistic: the facilitator can persist in absence of the facilitated predator, and the presence of the latter has a strongly negative effect on the equilibrium density of the former.

Our results show that the effects of within-species life-history processes can trickle up or down to other trophic levels, and result in highly counterintuitive effects. Facilitation as an emergent phenomenon of prey life-history characteristics offers a new mechanism that can perhaps contribute to understanding the structure and dynamics of ecological communities.

### 6.2 Model Analysis

To analyze the possibility of coexistence and facilitation, we model a consumer consisting of two life stages: Juveniles $J$ and adults $A$. Two predators $Q$ and $P$ each feed exclusively on juveniles ($J$) or adults ($A$) respectively. The system

\[
\begin{align*}
\frac{dJ}{dt} &= \beta A - \frac{J}{(1 + J^2)} - \mu_J J - QJ \quad (6.1a) \\
\frac{dA}{dt} &= \frac{J}{(1 + J^2)} - \mu_A A - A P \quad (6.1b) \\
\frac{dQ}{dt} &= Q (mJ - \nu) \quad (6.1c) \\
\frac{dP}{dt} &= P (\varepsilon A - \delta) \quad (6.1d)
\end{align*}
\]

describes the dynamics of these three species. The hump-shaped maturation function $J/(1 + J^2)$ regulates the consumer population in absence of predation. Maturation first increases with juvenile density, but decreases at high density. We assume that maturation is linked to size rather than age, and the maturation function is a reflection of this assumption. At low juvenile density, maturation is not limiting. We assume that when the density increases, juvenile growth slows down due to exploitation competition, which in turn slows down the maturation process. Adults produce juveniles at a rate $\beta$. Death rates for juveniles and adults are $\mu_J$ and $\mu_A$ respectively. Predator $Q$ feeds on juveniles at a rate $m$, while $P$ feeds on
Figure 6.1: A timeseries produced by system [6.1], started in the consumer-only equilibrium. At $t = 100$ the predator $P$ is introduced, but dies out immediately. At $t = 200$, juvenile predator $Q$ successfully invades, which induces dramatic changes in the structure of the consumer population. At $t = 400$ the predator $P$ invades once more, and establishes a new (all-species) equilibrium. Then at $t = 600$ the predator $Q$ is removed, which leads to rapid extinction of $P$ (illustrating the emergent facilitation effect discussed in the text), after which the consumer population returns to the original equilibrium. Parameter values for this run are $\beta = 0.5$, $\mu_J = 0.01$, $\mu_A = 0.05$, $\nu = 0.3$, $\delta = 1.0$, $m = n = 0.4$. 

adults at a rate $\varepsilon$. They die at rates $\nu$ and $\delta$ respectively. Note that this model is scaled to minimize the number of parameters. The unscaled model and the scaling procedure we used are described in the appendix.

The facilitation of predator $P$ by predator $Q$ is visualized in the timeseries of the model shown in figure 6.1. From $t = 0$ to 100, no predators are present, and the consumer population is at equilibrium density. At $t = 100$, the adult-specific predator ($P$) is introduced, but quickly dies out, after which the system returns to the consumer-only equilibrium, which demonstrates the absence of a
stable consumer-$P$ equilibrium. At $t = 200$, we introduce the other predator, $Q$, which successfully establishes itself. Consequently, the density of juvenile consumers ($J$) decreases, but the density of adult consumers ($A$), increases more than an order of magnitude. At $t = 400$ we once more introduce $P$, which successfully invades, and thereby significantly reduces the density of its beneficiary, the juvenile-specific predator $Q$. Finally, at $t = 600$, predator $Q$ is removed from the system, resulting in the immediate demise of $P$, after which the system returns to the consumer-only equilibrium. The phenomenon, that the adult-specific predator $P$ can persist only as a result of the shift in the distribution of the prey species, which is induced by its competitor $Q$, is the key issue of the current study.

One of the requirements for emergent facilitation to occur is that the predator $Q$ increases the equilibrium density of the adult consumer stage $A$, which forms the prey of the other predator, $P$. To this end we consider the consumer population in absence of predation ($P = Q = 0$). This allows us to calculate the equilibrium density of $J$. If we set equation [6.1b] equal to zero, we obtain an expression for the consumer-only equilibrium density of $A$, which we can substitute into equation [6.1a]. Solving for $J$ then yields the equilibrium density of juvenile consumers

$$J^c = \sqrt{\frac{1}{\mu_j} \left( \frac{\beta}{\mu_A} - 1 \right) - 1}. \quad (6.2)$$

If we consider the juvenile predator $Q$ as a constant, its effect (as long as $P = 0$) translates into an increase in juvenile prey mortality (since $-\mu_j J - Q J = -J (\mu_j + Q)$ in equation [6.1a]). It is immediately clear that the effect of the predator $Q$ is rather straightforward: As $Q$ increases from zero, the juvenile equilibrium density asymptotically approaches zero (consider substitution of $\mu_j$ by $(\mu_j + Q)$ in equation [6.2]). Consequently, $Q$ always has a negative effect on the equilibrium density of the prey stage on which it feeds. Because the maturation function is hump-shaped, a reduction in the juvenile density can lead to either an in- or decreased equilibrium adult consumer density $A$. Our model is scaled such that the maximum of the maturation function occurs at $J = 1$, so that the effect of predation by $Q$ will increase the equilibrium density of adult consumers when $J^c > 1$, and decrease it otherwise. In the former case, facilitation is in principle possible: Predation by $Q$, feeding on juveniles, can increase the consumer density in the other stage, $A$. For the adult predator $P$, VanKooten et al. (2003)(chapter 5 in this thesis) prove that for any set of parameter values, the equilibrium density of juvenile consumers $J$ is always lower when $P$ is present than when it is absent, and thus predator $P$ can never facilitate predator $Q$. Consequently, emergent mutualism, where each predator can persist only in the other's presence, is not possible. The effect of predator $P$ on the equilibrium density of its prey stage $A$ is less straightforward. By feeding on consumer stage $A$, predator $P$ reduces its density directly. However, it thereby also reduces reproduction and thus recruitment into the juvenile stage $J$, reducing the equilibrium density in that stage. When $J > 1$, such a decrease in density leads to increased maturation, and increased inflow into the mature consumer stage $A$. Hence, predator $P$ can increase the density of its
own prey by feeding on it. A detailed mathematical analysis of this phenomenon is given in De Roos et al. (2003b). The autocatalytic effect of predator $P$ increases the parameter range where it can persist. However, it can persist only if its density is above a certain threshold. Below this threshold the impact of $P$ on the population distribution of its prey is not sufficient to bring about the decrease in $J$ and increase in $A$ required for its persistence. In other words, the predator population shows positive density dependence at low density, also known as an Allee effect, which comes about through shifts that it induces in the prey population distribution.

Both the emergent Allee effect and the emergent facilitation can be observed in figure 6.2, which shows the equilibrium density of the two predators in relation to $\delta$, the mortality of the adult-specific predator $P$. We first consider only the consumer-$P$ equilibrium, which is represented by the thick solid and dashed lines. At mortality rates close to zero, the equilibrium density of the predator is limited by the availability of prey, and is thus largely independent of mortality. However, as $\delta$ is increased, the equilibrium density of $P$ slowly decreases. At a certain mortality value (around $\delta = 0.16$, solid line in figure 6.2), an alternative stable state of the system emerges. In the latter state the predator density is low, and the con-

![Figure 6.2: the equilibrium densities of the predator species $P$ and $Q$ in relation to $\delta$, the mortality of predator $P$. Thick solid and dashed lines: consumer-$P$ equilibrium. Thin solid line: all-species equilibrium. Dot-dashed line: Consumer-$Q$ equilibrium. Parameter values: $\beta = 0.5$, $\mu_J = 0.01$, $\mu_A = 0.05$, $\nu = 0.15$, $m = n = 0.4$.](image-url)
Figure 6.3: the bifurcation of the model with respect to predator properties. In the shaded area, emergent facilitation occurs. At low values of $\delta$, the consumer-$P$ equilibrium is stable, and at higher values, $P$ is extinct and the consumer-$Q$ equilibrium is stable. Parameter values: $\beta = 0.5$, $\mu_J = 0.01$, $\mu_A = 0.05$, $m = n = 0.4$.

Consumer density is hardly affected by the predator. The properties of this state are discussed in more detail in VanKooten et al. (2003) (chapter 5 in this thesis), and are hence not further discussed here. Its appearance co-occurs with the appearance of a threshold value in predator density that separates the two equilibria (the dotted line in figure 6.2). As $\delta$ increases further, the threshold density increases, until eventually it coincides with the predator's equilibrium density. At higher mortality, a consumer-$P$ equilibrium is no longer feasible, and increasing predator mortality beyond this point results in a sudden extinction ('catastrophic collapse', sensu VanKooten et al., 2003) of the adult-specific predator population. This extinction is not simply reversible by a small reduction of the predator mortality. To return the system to the original high $P$-density equilibrium, the mortality rate has to be decreased below $\delta \approx 0.16$, where there is no threshold density for $P$.

If we now consider the all-species (consumer-$P$-$Q$) equilibrium (the thin solid line in figure 6.2), emergent facilitation is prominently present: The all-species equilibrium spans a wide range of $\delta$ values, from below the extinction threshold of $P$ in absence of $Q$ (around $\delta = 0.3$) up to $\delta = 2.63$. In the presence of its
competitor $Q$, the maximum mortality rate at which the adult-specific predator $P$ can persist shifts from $\pm 0.45$ to $\pm 2.63$, a 5-fold increase. The range at which the juvenile-specific predator $Q$ can persist is bounded at low $\delta$ by the effect of its competitor $P$ on the juvenile consumer stage. When $\delta$ is very low, $P$ reduces the equilibrium density of $J$ to a level that is too low for $Q$ to persist. The value of $\delta$ where the consumer-P equilibrium destabilizes and the all-species equilibrium stabilizes is the point where $\bar{J} = \frac{\nu}{m}$, and hence equation [6.1c] changes sign (for $Q \geq 0$). With increasing $\delta$, the density of $Q$ in the all-species equilibrium gradually increases, while $P$ becomes less abundant. Eventually, at $\delta_{\text{max}}$, $P$ goes extinct. The value of $\delta_{\text{max}}$ can be calculated analytically by substitution of the equilibrium values $\bar{J} = \frac{\nu}{m}$ and $\bar{A} = \frac{\delta}{\varepsilon}$ into equation [6.1b]. By setting $P = 0$, we obtain an expression for $\delta$ where the predator $P$ goes extinct:

$$\delta_{\text{max}} = \frac{\varepsilon}{\mu_A} \frac{\nu m}{m^2 + \nu^2}$$  \hspace{1cm} (6.3)

When $\delta \geq \delta_{\text{max}}$, the consumer-$Q$ equilibrium is stable, and the density of $Q$ does not change anymore. In addition to increasing the persistence range of $P$, the emergent facilitation cancels the risk of a sudden extinction of the predator $P$, by facilitating a bypass to avoid the sudden disappearance of the consumer-$P$ equilibrium at $\delta = 0.45$ in figure 6.2. Starting from a predator-$P$ equilibrium at low $\delta$, a predator population that suffers increasingly strong mortality will eventually reach the point where the threshold density (dotted line in figure 6.2) coincides with the equilibrium density, at which point predator $P$ will go extinct. As described above, this change is not simply reversible. It can only be reversed by decreasing $\delta$ to much lower values. In the presence of $Q$ however, the point where $P$ suddenly goes extinct is never reached when $\delta$ increases. Instead, at a certain value of $\delta$, predator $Q$ can invade. When $\delta$ increases further, the equilibrium density of $P$ smoothly decreases, while that of $Q$ increases. When $\delta$ is decreased, it the opposite happens, until eventually the density of $Q$ becomes zero, and the consumer $P$ equilibrium is reinstated.

The presence or absence of emergent facilitation does not crucially depend on the exact specifications of the juvenile predator $Q$. The shaded area in figure 6.3 shows the combinations of $\nu$ and $\delta$, the mortality rates of predators $Q$ and $P$ respectively, for which $P$ can only persist in the presence of $Q$, and hence emergent facilitation takes place. It occurs for a wide range of mortality rates $\nu$ of predator $Q$, but is strongest around $\nu = 0.5$. It is limited on one side by the stability boundary of the consumer-$P$ equilibrium. At lower values of $\delta$, $P$ can persist in absence of $Q$ and even outcompete $Q$. At low $\nu$ this boundary curves towards the origin, reducing the range of $\delta$ for which the consumer-$P$ equilibrium is stable. At high $\delta$, the area of emergent facilitation is limited by the point $\delta_{\text{max}}$ (equation [6.3]), where predator $P$ goes extinct despite the presence of $Q$. Beyond this boundary, only the consumer-$Q$ equilibrium is stable. Eventually, at $\nu = 12$ (not shown), the juvenile-specific predator $Q$ reaches its extinction threshold. At higher values of $\nu$, it can not persist, and hence no facilitation of $P$ is possible.
Whether or not emergent facilitation can occur depends not only on the characteristics of the predators. The properties of the prey are equally important. Figure 6.4, illustrates the effects of \( \mu_j \), the mortality of the juvenile consumers and \( \delta \) on the occurrence of the consumer-\( P \), consumer-\( Q \) and the all-species equilibria. At low \( \delta \), the consumer-\( P \) equilibrium is the only stable equilibrium. This means that if a consumer-\( Q \) equilibrium in this parameter range is invaded by \( P \), predator \( Q \) goes extinct. In the parameter space marked 'stable all-species equilibrium' in figure 6.4, the consumer-\( P \) equilibrium is unstable to invasion by \( Q \), but it does exist. Hence, if we would artificially remove predator \( Q \) from the system, predator \( P \) would still persist. At even higher \( \delta \), the consumer-\( P \) equilibrium eventually disappears altogether, while the all-species equilibrium still exists. In this region of parameter space (the shaded area in figure 6.4), emergent facilitation occurs. If we remove predator \( Q \) from the system, \( P \) swiftly goes extinct, as illustrated in figure 6.1. This region is bounded by the maximum mortality rate \( \delta_{\text{max}} \) (equation [6.3]) that predator \( P \) can sustain, which is independent of juvenile mortality \( \mu_j \). The parameter range over which emergent facilitation occurs diminishes when

![Figure 6.4: The stability of the consumer-\( P \), consumer-\( Q \), and all-species equilibrium, and the presence of emergent facilitation in relation to \( \mu_j \), the mortality of juvenile consumers, and \( \delta \), the mortality of the adult-specific predator \( P \). The shaded area indicates the parameter values for which predator \( P \) can occur only in the presence of the juvenile predator \( Q \), and hence emergent facilitation occurs. Parameter values: \( \beta = 0.5 \), \( \mu_A = 0.05 \), \( \nu = 0.15 \), \( m = n = 0.4 \).]
$\mu_j$ is increased. An important conclusion from figure 6.4 is that emergent facilitation can only occur at low to intermediate juvenile mortality values, since the phenomenon crucially depends on the stability of the all-species equilibrium. An increase in the birth rate of the consumer ($\beta$), enlarges the range of $\mu_j$ where the all-species equilibrium is stable, leading us to conclude that emergent facilitation is more likely to occur in systems where the prey species has high fecundity and/or low juvenile mortality.

### 6.3 Discussion

In this study, we show that in a system where two predators compete for a shared prey, but feed on different life stages of the prey, one predator can facilitate its competitor through its effect on the prey density and stage distribution. By reducing the density in the regulating stage of the prey, the juveniles in our case, competition in this prey stage is released, which leads to increased development and maturation from this stage. Hence, feeding by the predator leads to higher density in the older prey stage(s), which is vulnerable to predation by a second predator species. Facilitation occurs when this density increase lifts the prey density for the second predator to values at which it can persist. This facilitation comes about purely through the numerical effect of the predator on its prey, and the life-history characteristics of the prey. Through this effect, coexistence between the predators occurs for a wide range of parameter values. The facilitation effect greatly expands the parameter range for which the facilitated predator can persist. The presence of the facilitated predator has an negative effect on the equilibrium density of the predator that enables the coexistence, and hence the interaction is not mutualistic. Furthermore, the interaction is asymmetrical in the sense that the predator feeding on adult prey can be facilitated by the predator feeding on the regulating prey stage (juveniles), but not vice versa.

Our results indicate that emergent facilitation occurs under a broad range of parameter values of both the predators and the prey species involved. It is most likely to occur for highly fecund prey species, but can also be found with less productive prey when background mortality in the regulating stage is low. In our system, the prey population is regulated in the juvenile stage, but an analysis of a model with more prey stages has revealed that the same results are obtained when the regulation occurs elsewhere, as long as it is in the maturation from one stage to another. On purely mathematical grounds, based on the wide range of parameter values under which it occurs, we expect emergent facilitation to be a fairly common phenomenon among predators that feed on different life-stages of a prey species with food- or density-dependent development.

De Roos and Persson (2002), De Roos et al. (2003b), and VanKooten et al. (2003) find that the adult predator $P$ runs the risk of a catastrophic collapse (sudden extinction) when its environment deteriorates, as a result of an emergent Allee effect. Emergent facilitation by a second predator can alleviate the risk of a catastrophic collapse of a population of top predators. The predator $Q$, feeding on the
juvenile consumer stage, acts as a 'helper species' in this respect. It increases the consumer density in the other stage, keeping the density high enough for the adult predator to re-establish itself. As long as the all-species equilibrium is connected to the consumer-$P$ equilibrium, such as in figure 6.2, there is no risk of an irreversible catastrophic collapse.

The great majority of species suffer predation from more than one predator species (Schoener, 1989; Polis, 1991). Classically, the competition between predators for a prey has been explained as either direct interference competition, or as exploitation competition, where one predator species indirectly reduces the density of a competitor, by directly reducing the density of a shared resource (Wootton, 1994). The negative outcome of the interaction - one competitor reducing the other's density, is an integral part of the exploitative competition concept. Positive interactions between two competitors can occur, but are generally thought to occur due to trait-mediated effects, where one predator induces a certain change in the state or behavior of its prey, thereby changing its susceptibility to a competing predator. Both negative (competition) and positive (facilitation) instances of such indirect effects between predators have been found (for references see reviews by Sih et al., 1998; Werner and Peacor, 2003). We show that positive interactions can emerge through population dynamical feedback, without any assumptions about trait-mediated effects. The emergent facilitation is strong enough to even reverse the type of interaction from negative (competitors) to positive (facilitation).

The potential for emergent facilitation to act in a particular system has important consequences in relation to conservation measures. Our results imply that such measures could potentially backfire. Culling one predator in order to increase food availability to a rare competitor could lead to the extinction of the latter species if it is facilitated by the first.

The facilitation we find is reminiscent of the dynamics which can be caused by intraguild predation (when one predator is also prey for the other predator) (Polis and Holt, 1992; Holt and Polis, 1997). In such a system, stable coexistence can occur when the intraguild predator is an inferior competitor compared to the intraguild prey. In this case, the intraguild prey (the competitor that acts as alternative prey to the intraguild predator) increases the range of conditions over which the intraguild predator can persist, while the intraguild prey density is strongly reduced Diehl and Feissel (2000). Intraguild predation explicitly assumes a positive effect of one competitor on the other (through the predatory interaction), while our results emerge from the prey population dynamics, without explicit positive interactions.

Already in 1972, Haigh and Maynard Smith express the idea that coexistence between competing parasitoids may be possible when the host is maturation- or production-regulated, and the parasitoids attack different life stages of the host. However, Briggs (1993) showed that in a system consisting of two parasitoids feeding on different stages of a host population, coexistence between parasitoids is restricted to a highly limited area of parameter space. The model analyzed by Briggs (1993) is inspired by biological control, where the most relevant research questions are related to whether or not the host can escape control by the para-
sitoids. Hence, Briggs (1993) modeled a prey population which is unregulated in absence of the predators. While this is a legitimate assumption in relation to biological control, the host population they studied could in principle be food- or density-limited in absence of the parasitoids. Our analysis indicates that such regulation can in principle have important consequences for coexistence of the parasitoids, but also for the equilibrium density and stage distribution of the host.

Vonesh and Osenberg (2003) studied the impact of two stage-specific predators on a shared prey, the African tree frog *Hyperolius spinigularis*. One predator feeds on the eggs, the other on the larval stage of the tree frog. They found that there is indeed a significant interaction between the predators, which stems from numerical responses of the prey. Reduced recruitment into the larval stage due to egg-predation caused a strong reduction in the efficiency of the larval predator, which appeared to be at least in part due to released intra-stage competition among the remaining larvae, resulting in faster growth of these larvae through the vulnerable size class. These tree frogs appear to exhibit density-limited development, and hence counterintuitive emergent effects such as facilitation between the predators could in principle occur, but this would require experiments that span multiple generations of the prey. A first indication of emergent facilitation in this system could be found in the growth rate of the egg predator. If facilitation occurs, we expect the egg predator to be unable to persist in the absence of the larval predator, because the competition in the larval stage would lead to strongly limited recruitment into the adult stage and hence to production of too few eggs to sustain a population of egg predators. The presence of larval predators could release the competition among juveniles, resulting in faster maturation and higher production of eggs, facilitating the egg predator.

Since the formulation of the competitive exclusion principle (Gause, 1934), ecologists have been trying to explain the high diversity of species observed in many systems given the limited number of resources available (Hutchinson, 1961; Chesson, 1986). A number of explanations have been advanced including extrinsically driven environmental variation (Hutchinson, 1961; Levins, 1979; Chesson, 1986, 2000b), intrinsically driven non equilibrium dynamics (Armstrong and McGehee, 1980) and spatial aggregation (Atkinson and Shorrocks, 1981; Chesson, 1991, 2000a). The bulk of literature on interspecific competition deals with interactions between species, and hence the indirect interaction of competitors through the life-history of a shared prey received little attention. Our study adds a new perspective to the discussion about coexistence of similar competitors. We show that within-species processes such as density-dependent development can lead to unexpected and counterintuitive interactions on the community level.
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6.5 Appendix: Model Scaling

The original model equations are as follows:

\[ \frac{dJ}{dt} = \beta A - \frac{\phi J}{(1 + dJ^2)} - \mu_J J - \alpha QJ \]  
\[ (6.4a) \]

\[ \frac{dA}{dt} = \frac{\phi J}{(1 + dJ^2)} - \mu_A A - \eta AP \]  
\[ (6.4b) \]

\[ \frac{dQ}{dt} = Q(\alpha \gamma J - \nu) \]  
\[ (6.4c) \]

\[ \frac{dP}{dt} = P(\eta \lambda A - \delta) \]  
\[ (6.4d) \]

To reduce the number of parameters, we have scaled this model. We multiplied the variables \( J \) and \( A \) by a factor \( \sqrt{d} \), and the time by a factor \( \phi \). Hence, all rate parameters \( \beta, \mu_J, \mu_A, \delta \) and \( \nu \) in the scaled model (equations [6.1]) are expressed as fractions of \( \phi \), the maximum maturation rate of juveniles at low population density. If we then substitute for the predators \( P \) and \( Q \) respectively \( P = \frac{\eta}{\phi} P \) and \( Q = \frac{\alpha}{\phi} Q \), we can introduce the new parameter complexes \( \varepsilon = \frac{n^2 \lambda}{\phi \sqrt{d}} \) and \( m = \frac{\alpha \gamma}{\phi \sqrt{d}} \), to get rid of the predator attack rates. Substitution of these variables leads, after shuffling of terms and consecutive introduction of newly defined parameter complexes, to the scaled model equations [6.1]. The analysis in this paper is conducted with the scaled model.