Original Research Article

Dynamics and coexistence in a system with intraguild mutualism

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ABSTRACT

It is a tenet of ecological theory that two competing consumers cannot stably coexist on a single limiting resource in a homogeneous environment. Many mechanisms and processes have since been evoked and studied, empirically and theoretically, to explain species coexistence and the observed biological diversity. Facilitative interactions clearly have the potential to enhance coexistence. Yet, even though mutual facilitation between species of the same guild is widely documented empirically, the subject has received very little theoretical attention. Here, we study one form of intraguild mutualism in the simplest possibly community module of one resource and two consumers. We incorporate mutualism as enhanced consumption in the presence of the other consumers. We find that intraguild mutualism can (a) significantly enhance coexistence of consumers, (b) induce cyclic dynamics, and (c) give rise to a bi-stability (a 'joint' Allee effect) and potentially catastrophic collapse of both consumer species.

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1. Introduction

Explaining coexistence of multiple species and finding mechanisms for the maintenance of biological diversity are two of the most fundamental questions in ecology, and are increasingly important issues in the face of global anthropogenic change and biodiversity loss. Theoretical results such as Tilman's R^*-rule (Tilman, 1982) and the generalized competitive exclusion principle (Levin, 1970) send the clear message that coexistence among competing species is difficult to achieve. For example, the R^*-rule says that the species that can drive the resource (R) to the lowest level will win the competition and exclude other species. Theoretical and empirical research has since focused on variability and trade-offs that promote coexistence, such as spatial extent, temporal variation, stochasticity and others, e.g. Levin and Culver (1971), Holt (1984), Chesson (1994), Hanski and Gilpin (1997), and Chesson (2000). Most of these efforts focus on models and experiments that consider only antagonistic interactions even though positive interactions also pervade in ecological communities (Boucher, 1982; Bruno et al., 2003). Positive interactions are a natural candidate mechanism to promote species coexistence, and have been found to enhance ecosystem function in various ways (Stachowicz, 2001; Cardinale et al., 2002; Xie et al., 2011). However, relatively little work has been done in this regard

especially for facilitation among animal species; much of the research has dealt with facilitation in plants (Callaway, 1995; Bertness and Leonard, 1997).

A form of facilitation of which very little is known is intraguild mutualism (Crowley and Cox, 2011), where consumers competing for the same resources also facilitate one another. The idea of intraguild mutualism goes back to Charnov et al. (1976), who theorized several mechanisms of predator mutual facilitatation. When different predator species hunt in different locations or at different times, then a prey trying to avoid one predator could be more available to another. Charnov et al. (1976) mentions how nocturnal predation by owls may drive prey to forage during daytime where hawks can spot them – and vice versa. Other examples are that mammals may hunt under dense cover and drive prey into the open where it is available for avian predators – and vice versa (Korpimäki et al., 1996; Eccard et al., 2008). Sublethal predation by fish on clams has been found to facilitate lethal predation by shorebirds and predatory whelks (Meyer and Byers, 2005).

In general, increased feeding success and predator avoidance are the most commonly cited potential benefits between otherwise competing species (Dickman, 1992). Losey and Denno (1998) measured predation rates of two beetle species on aphids and showed that joint predation was greater than individual predation combined. Similar results of facilitation between predators were obtained, for example, by Cardinale et al. (2003), Meyer and Byers (2005), Bshary et al. (2006), Eccard et al. (2008), and Fodrie et al. (2008) in a wide variety of study systems. The mutual positive

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effect of predator defense or avoidance is documented by Hay (1986), Hoeck (1989), among others.

A recent review by Crowley and Cox (2011) highlights the current increase in recognition of the importance and ubiquity of facilitative interactions in ecology, see also Bruno et al. (2003). Specifically, they argue that there is ample empirical evidence for facilitative interactions and mutualism (reciprocal facilitation) within a guild, but that theoretical models of intraguild mutualism are rare. Stanton (2003) used path analysis to explore how pairwise mutualistic interactions affect systems of more than two species. Gross (2008) focused on the aspect of predator avoidance and studied a differential equations model of competing species whose death rates decrease in the presence of other species. He found that this mechanism produced stable multi-species communities with a single resource. Holland and DeAngelis (2009) consider a general two-species model where density-dependent rates can shift competitive interactions to mutualism, but the authors neither consider specific mechanisms nor address intraguild mutualism.

Here, we develop and analyze a model of resource competition, where consumption of each competitor can be enhanced by the presence of the other. Crowley and Cox (2011) suggest several community modules of varying topology, in which the effects of intraguild mutualism should be explored. Our work aims to shed light onto these effects in the most basic module, that of one resource and two competing consumers. By focusing on the most basic module, we isolate the fundamental processes of intraguild mutualism in order to thoroughly understand them and establish foundations for further inquiry. Our model consists of three equations, one for the resource and two for the consumers. We distinguish between two scenarios, the *chemostat scenario*, which is characterized by a constant supply rate of the resource and equal wash-out rates for all three species (Smith and Waltman, 1995); and the *logistic scenario*, which is characterized by a logistically growing resource population and species-specific death rates. Our approach to understanding the dynamics of this three-dimensional system begins with simple linear predation and facilitation functions, and considers two special cases of parameter values. When the two consumers are identical, the system reduces to a two-dimensional model of a predator with self-facilitation (Section 3). When facilitation acts in one direction only, the system remains three-dimensional but the number of parameters is greatly reduced (Section 4). These two special cases help understand the dynamics of the general system, but they are worthy of study in their own right, as both of these cases are observed in nature. Finally, we briefly discuss the effect of nonlinear predation and facilitation functions (Section 5), and we construct the possible dynamics of the full three-dimensional model from the results of the two previous sections (Section 6).

2. Model

We model the dynamics of two consumer species, x, y, and their resource, z. In the absence of the consumers, the resource grows according to some function G. Consumers per-capita catch rates are $h_i(z)$, modified to include consumer mutualism via functions f_i. There are linear death rates, d_i, of the consumers and yields $1/e_i$. Altogether, the model reads

$$
\begin{aligned}
\dot{x} &= x(h_1(z)f_1(y) - d_1), \\
\dot{y} &= y(h_2(z)f_2(x) - d_2), \\
\dot{z} &= G(z) - e_1 x h_1(z) f_1(y) - e_2 y h_2(z) f_2(x).
\end{aligned} \tag{1}
$$

We distinguish two scenarios. In the *chemostat scenario*, we consider $G(z) = d(z_{in} - z)$ as the supply rate and outflow of the

resource, and $d_1 = d_2 = d$ as the outflow rate of the consumers. In the *logistic scenario*, we choose logistic growth $G(z) = rz(1 - z/K)$, and we allow the consumer death rates d_i to be distinct. Parameters z_{in}, r, and K are the inflow concentration, the growth rate and the carrying capacity of the resource, respectively. We also refer to the consumers as predators. While we do not claim that all of the above mentioned facilitation mechanisms occur in a true chemostat, we suggest that the chemostat scenario, because of its simplicity, provides useful insights into the fundamental process of facilitation in isolation of any confounding factors.

The functions h_i describe a non-decreasing functional response; they could be linear or saturating (type II) (Holling, 1959). Functions f_i model facilitation if $f_i > 1$. We assume that $f_i(0) = 1$ and that these functions are non-decreasing. For (mathematical) simplicity, we consider linear functions where the strength of facilitation is proportional to the density of the facilitating population. We also discuss the case of saturating functions, where each additional competing consumer has a smaller facilitative effect and where the total possible positive effect is bounded above. In reality, it is likely that at very high densities of a competing consumer the facilitative effect decreases. Similarly, one could include self-facilitation by allowing functions f_i to depend on some linear combination of densities of the two species. We leave this case for future studies.

With constant functions $f_i = 1$, we have a classical situation. There is no stable coexistence, unless the two species have the same 'break-even concentrations' for the resource (Kot, 2001). In the chemostat case, the species that can subsist on a lower resource level will drive the other to extinction. The lowest possible resource level is given by $h_i(z) = d_i$. In the logistic case, the same relation holds unless there are limit cycles. Coexistence between the predators may be obtained along a stable limit cycle, provided at least one of the h_i are saturating response functions (Koch, 1974; Armstrong and McGehee, 1980; Kot, 2001).

3. Identical consumers – reduced system

We begin our analysis of system (1) with the special case that all parameters for the two consumer species are equal. With this assumption, the plane $\{x = y\}$ is invariant for the dynamics. On this plane, the dynamics are completely determined by the reduced system

$$
\begin{aligned}
\dot{x} &= x(h(z)f(x) - d), \\
\dot{z} &= G(z) - 2exh(z)f(x).
\end{aligned} \tag{2}
$$

where the factor of 2 in the last term reflects the fact that two consumer species of equal strength impact the resource. System (2) has an alternative interpretation as a two-species predator–prey model with predator intra-specific facilitation and can be studied in its own right. In that interpretation f quantifies the facilitative effect of predator x on itself, and the yield is $1/(2e)$. Predator self-facilitation is quite common when predators hunt in packs, as in many canids. It also appears to be widespread in consumer–resource relationships in general, having been observed in terrestrial invertebrates (So and Dudgeon, 1989), aquatic invertebrates (Bertness, 1989) and parasites (Ogden et al., 2002). We refer to Berec (2010) for a recent in-depth study of the dynamic effects of self-facilitation in predators. For our model, we study the stability of the resource-only (semi-trivial) state as well as conditions for the existence and stability of a (positive) coexistence state.

3.1. The chemostat scenario

In the chemostat case, we choose $G(z) = d(z_{in} - z)$, as well as linear functions $h(z) = az$ and $f(x) = 1 + \alpha x$. After nondimensionalizing

$x = \tilde{x}d/(2ae), z = \tilde{z}z_{\rm in}$ and $t = \tilde{t}/d$ and dropping the tildes for convenience, the system reads

$$\dot{x} = x(Az(1 + Cx) - 1),$$
$$\dot{z} = 1 - z - xz(1 + Cx), \tag{3}$$

where $A = az_{\rm in}/d$ and $C = d\alpha/(2ea)$. The semi-trivial state is unstable if $A > 1$. A coexistence state is given by the relations

$$z = \frac{1}{A(1 + Cx)}, \qquad Cx^2 + (1 - AC)x + 1 - A = 0. \tag{4}$$

The explicit solution for x is

$$x = \frac{1}{2C}\left[AC - 1 \pm \sqrt{(AC - 1)^2 - 4C(1 - A)}\right]. \tag{5}$$

Now we see that there are three cases. (a) If $A > 1$, then the zero steady state is unstable; there is exactly one coexistence state. (b) If $A < 1$ and $AC < 1$ then there are no coexistence states. (c) If $A < 1$ and $AC > 1$, then there are two coexistence states, provided the expression under the square root is positive. The latter condition is equivalent to

$$C > C^* = \frac{1}{A^2}\left[2 - A + 2\sqrt{1 - A}\right], \tag{6}$$

which actually implies $C > 1/A$. We also get the relationship $(1/A)x + z = 1$.

The Jacobian at the positive steady state is

$$J = \begin{bmatrix} ACxz & x/z \\ -z(1 + 2Cx) & -1/z \end{bmatrix}. \tag{7}$$

It turns out that the trace of the Jacobi matrix is always negative at the positive steady state. When $A > 1$, this is easily seen from

$$\mathrm{tr}(J) = ACxz - \frac{1}{z} = \frac{Cx}{1 + Cx} - A(1 + Cx) < (1 - A)Cx < 0. \tag{8}$$

For $A < 1$, we checked the condition numerically. In particular, there cannot be a Hopf bifurcation in this system. The sign of the determinant depends on the steady state. We have

$$det(J) = x(1 + 2Cx - AC). \tag{9}$$

Substituting the explicit expression for x from (5), we see that the determinant is positive (a) if $A > 1$ and $x > 0$ or (b) if $A < 1$ and x is the larger of the two positive steady states.

Mathematical summary: When $A > 1$, then the semitrivial steady state is unstable and the unique coexistence state is stable. When $A < 1$ and $C < C^*$, then the predator cannot persist in the system. When $A < 1$ and $C > C^*$, then the semitrivial state is locally stable and there are two coexistence states. The one with the larger consumer density is stable. The consumer experiences a strong Allee effect, i.e. a small initial population of consumers will die out and only a sufficiently large initial consumer density will guarantee persistence (Allee, 1949), see Fig. 1.

Biological summary: If the catch rate of the consumer is large enough to ensure persistence in the absence of facilitation, then facilitation will not change the behavior qualitatively. A small population will grow to a stable steady state; only it will grow faster and to a higher steady state value with facilitation. If the catch rate of the consumer is too small to sustain the population in the absence of facilitation, then a strong enough facilitative effect can help the population persist, but only if the population density is high enough initially.

3.2. The logistic scenario

This time, we choose $G(z) = rz(1 - z/K)$, and h, f as in the previous section. After nondimensionalizing $x = \tilde{x}r/(2ae), z = \tilde{z}K$
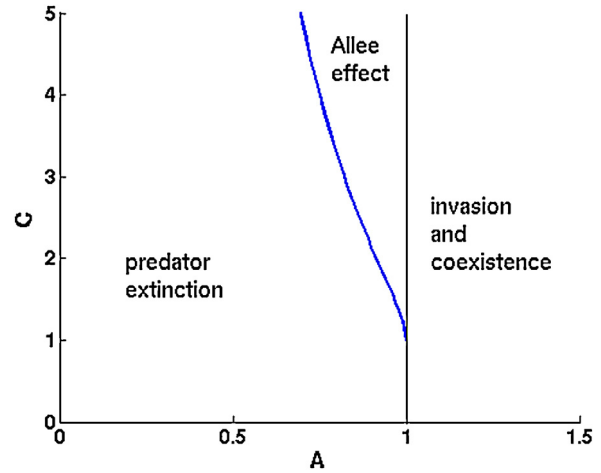
Fig. 1. Illustration of the possible qualitative behavior of the reduced mutualism model with chemostat dynamics, see (2). When the catch rate (A) is large enough consumers can invade and coexist. When the catch rate is too small but mutualism (C) is strong enough then we observe an Allee effect; the predator will go to extinction from small initial density.

and $t = \tilde{t}/r$ and dropping the tildes for convenience, system (2) reads

$$\dot{x} = x(Az(1 + Cx) - B),$$
$$\dot{z} = z(1 - z) - xz(1 + Cx), \tag{10}$$

where $A = aK/r$, $B = d/r$ and $C = r\alpha/(2ea)$. The semi-trivial state is unstable when $A > B$. A coexistence state satisfies the cubic equation

$$C^2x^3 + 2Cx^2 + (1 - C)x + \frac{B}{A} - 1 = 0, \tag{11}$$

and $z = B/(A(1 + Cx))$. When $A > B$, then the cubic polynomial has exactly one positive root by Descartes' rule of signs. When $A < B$, then there are zero or two positive roots. By Descartes' rule again, we need $C > 1$ for there to be two positive roots. If $C > 1$, then a saddle-node bifurcation occurs at

$$A^* = \frac{B}{1 + (-4 + 2\sqrt{1 + 3C})/9C(C - (\sqrt{1 + 3C}/3 - (1/3)))}, \tag{12}$$

so that the system has two positive steady states whenever $A \in (A^*, B)$.

At a positive steady state, the Jacobi matrix can be reduced to

$$J = \begin{bmatrix} ACxz & Bx/z \\ -z(1 + 2Cx) & -z \end{bmatrix}. \tag{13}$$

The trace of this matrix is zero if $x = 1/AC$. Substituting this expression into the steady state equation (11), we obtain a curve in parameter space on which a Hopf bifurcation can occur, provided the determinant is positive there, namely

$$C^{**} = \frac{1 + 2A + A^2}{A^3 + (1 - B)A^2}. \tag{14}$$

Mathematical summary: When $A > B$, then the semitrivial steady state is unstable. The unique coexistence state is stable when $C < C^{**}$ and unstable with a stable limit cycle when $C > C^{**}$. When $A < B$, the situation is more complex. When C is small, then the predator cannot persist in the system. As C increases, there is a saddle node bifurcation, whereby a stable and unstable coexistence state emerge. Implicitly, the critical value of C is given by
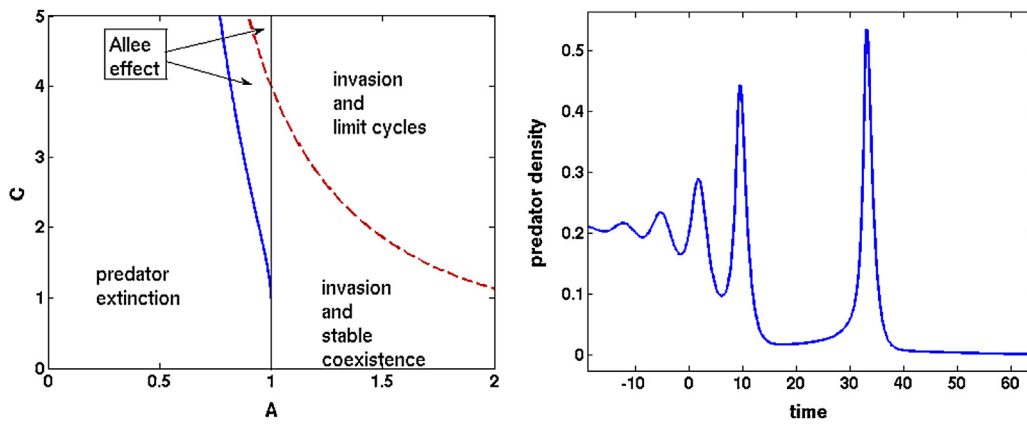
Fig. 2. Illustration of the possible qualitative behavior of the reduced mutualism model with logistic dynamics as a function of catch rate (A) and strength of mutualism (C). (Left) Bifurcation diagram for death rate $B = 1$. To the right of the vertical line, the predator can invade and coexist. To the left of the vertical line, the zero state of the predator is locally stable. The predator has an Allee effect above the solid curve. At the dashed curve, the coexistence state undergoes a Hopf bifurcation, so that there is bistability between the extinction state and a limit cycle. For even larger values of C, the population can crash (region not shown). (Right) The coexistence state is an unstable focus; the oscillations in the predator density grow and eventually fall below the Allee threshold so that the predator becomes extinct. Parameters are $A = 0.9$, $B = 1$, and $C = 9$.

(12). Increasing C further causes a Hopf bifurcation when $C = C^{**}$ at the larger coexistence state and the appearance of a stable limit cycle; see Fig. 2. For very large values of C, the limit cycle disappears in a global bifurcation. More precisely, as the limit cycle grows, it approached the saddle point and becomes a homoclinic orbit at the bifurcation point. As that happens, the predator goes extinct; see Fig. 2.

Biological summary: Strong enough facilitation can destabilize the positive predator steady state and introduce oscillations. If the predator catch rate is high enough to survive in the absence of facilitation, then oscillations will remain bounded and the predator will persist. If the predator catch rate in the absence of facilitation is too low for persistence, then, as before, an Allee effect can emerge for strong enough facilitation. In that case, strong facilitation can lead to large oscillations, which, in turn, can push the predator below the Allee threshold and consequently to extinction. Hence, facilitation is not necessarily beneficial for the population.

4. Facilitation – reduced system

Another very instructive way to reduce the complexity of model (1) is to assume that only one species facilitates resource uptake for the other. There is abundant empirical evidence for such interactions in natural systems, particularly between birds and a variety of terrestrial and marine taxa; see Kajiura et al. (2009) and references therein. For example, double-crested cormorants (*Phalacrocorax auritus*) have been observed to feed on fish flushed out of hiding, but not consumed, by foraging southern stingrays (*Thalassia testudinum*). Already Charnov et al. (1976) mentions that the Rufous Babbler (*Pomatostomus iridorei*), while foraging for other food, flushes insects which it does not eat but which are then eaten by other species.

Our setup is as follows. We assume that species x has the lower R^* value in the sense of Tilman (1982), so that it wins the competition in the absence of facilitation. We then assume that species y benefits from the presence of x but not vice versa. We start with the chemostat scenario.

4.1. The chemostat scenario

We choose the functions G, h_i, f_i of model (1) as in Section 3.1, with $f_1 = 1$. After non-dimensionalizing $x = \tilde{x}d/(2a_1e_1), y = \tilde{y}d/(2a_2e_2),$

and z, t as in (3), and dropping the tildes for convenience, we obtain

$$\begin{aligned}
\dot{x} &= x(A_1z - 1), \\
\dot{y} &= y[A_2z(1 + Cx) - 1], \\
\dot{z} &= 1 - z - z[x + (1 + Cx)y],
\end{aligned} \quad (15)$$

where $A_i = a_iz_{in}/d$, and $C = \alpha d/e_1a_1$. The condition that species x has a lower R^* value than species y translates into $A_1 > A_2$.

The resource-only steady state $(0, 0, 1)$ is invasible by x if $A_1 > 1$ and by y if $A_2 > 1$. If $A_2 > 1$, then x can invade the semi-trivial state $(0, A_2 - 1, 1/A_2)$ since $A_1 > A_2$ by assumption. If $A_1 > 1$, then y can invade the semi-trivial state $(A_1 - 1, 0, 1/A_1)$ provided

$$C > C^* = \frac{(A_1/A_2) - 1}{A_1 - 1}. \quad (16)$$

In particular, species y can invade if facilitation by species x is strong enough. If the invasion conditions are satisfied, the coexistence state is given explicitly by the expressions

$$x = \frac{1}{C}\left(\frac{A_1}{A_2} - 1\right), \quad y = \frac{A_2}{A_1}(A_1 - 1) + \frac{1}{C}\left(\frac{A_2}{A_1} - 1\right), \quad z = \frac{1}{A_1}, \quad (17)$$

see Fig. 3. We show that this unique coexistence state is stable when it exists. The Jacobian at the coexistence state reads

$$J = \begin{bmatrix} 0 & 0 & A_1x \\ A_2Cyz & 0 & A_1y \\ -z(1 + Cy) & -1/A_2 & -A_1 \end{bmatrix}. \quad (18)$$

Since all coefficients of the characteristic polynomial are positive, the Routh–Hurwitz conditions for stability reduce to

$$A_1y + A_2x > A_2Cxyz(1 - A_1). \quad (19)$$

Since the coexistence state only exists if $A_1 > 1$, this condition is always satisfied. We illustrate the coexistence region in terms of C versus A_2 in Fig. 3 for two different values of A_1. Surprisingly, the two curves intersect. When $A_2 < 1$, the strength, C, with which species x has to support species y to enable persistence decreases as A_1 increases. There are two opposite effects at work. Higher A_1 implies lower resource level ($1/A_1$) at which species y tries to invade, so that we expect a *higher* value of C would be necessary. However, with increasing A_1, the steady state level of species x also increases, and the facilitation that species y receives from this increased density more than compensates for the lower resource
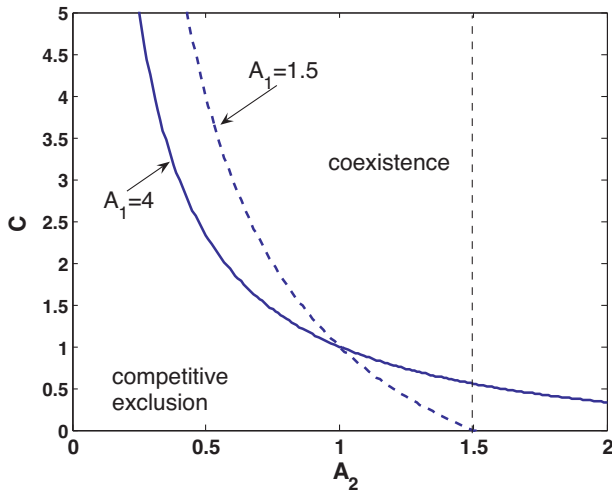
Fig. 3. Coexistence region of both consumers with facilitation in the chemostat scenario. Stable coexistence between all three species occurs above the curve, when facilitation (C) and catch rate of the inferior consumer (A_2) are large enough. Below the curve, species x exclude species y from the system. The assumption that species x is competitively superior implies that $A_2 < A_1$, so the values of A_2 are restricted to the region to the left of the dashed vertical line in the case $A_1 = 1.5$.

level. In fact, differentiating the expression in (16) with respect to A_1 shows that C increases with A_1 if and only if $A_2 > 1$.

Biological summary: In this scenario, the competitively inferior species (in the absence of facilitation) can invade when rare and coexist stably with the superior species provided the superior species offers some facilitation. In fact, strong enough facilitation can even allow for persistence of an inferior competitor that would go extinct in the absence of the superior competitor/facilitator. If the inferior competitor can persist by itself in the absence of competition ($A_2 > 1$), then the level of facilitation required from the superior competitor increases with the catch rate of the superior competitor. If the inferior competitor cannot persist by itself, then the level of facilitation by the superior competitor required for species y to coexist is much higher overall, but it is decreasing with the catch rate of the superior competitor.

4.2. The logistic scenario

With logistic growth for the prey, the nondimensional equations ($x = \tilde{x}r/(2a_1e_1)$, $y = \tilde{y}r/(2a_1e_1)$, z, t as in (10)), read

$$
\begin{aligned}
\dot{x} &= x(A_1 z - B_1), \\
\dot{y} &= y[A_2 z(1 + Cx) - B_2], \\
\dot{z} &= z(1 - z) - z[x + (1 + Cx)y],
\end{aligned}
\tag{20}
$$

where $A_i = a_i K/r$, $B_i = d_i/r$ and $C = \alpha r/(e_1 a_1)$. Species x outcompetes species y if $(A_1/B_1) > (A_2/B_2)$. We introduce the notation $R_i = B_i/A_i$, so that the assumption about x being the stronger competitor gives Tilman's R^*-rule $R_1 < R_2$ (Tilman, 1982).

The prey-only state $(0, 0, 1)$ is invasible by x if $A_1 > B_1$ and by y if $A_2 > B_2$. Species x invades the semi-trivial state $(0, 1 - R_2, R_2)$ since $R_2 > R_1$. Species y invades the semi-trivial state $(1 - R_1, 0, R_1)$ only if

$$
C > C^* := \frac{(R_2/R_1) - 1}{1 - R_1}.
\tag{21}
$$

Under this condition, the coexistence state is given explicitly by the expressions

$$
x = (1 - R_1)\frac{C^*}{C}, \quad y = \frac{R_1}{R_2}(1 - R_1)\left(1 - \frac{C^*}{C}\right), \quad z = R_1.
\tag{22}
$$

All expressions are positive by assumption.

The Jacobi matrix at the coexistence state is

$$
J = \begin{bmatrix}
0 & 0 & A_1 x \\
A_2 C R_1 y & 0 & \dfrac{B_2}{R_1} y \\
-R_1(1 + Cy) & -R_2 & -R_1
\end{bmatrix}.
\tag{23}
$$

The only condition of the Routh–Hurwitz criteria for stability that is not automatically satisfied is

$$
A_1 C R_1 xy + A_1 R_1 x + \frac{B_2 R_2 y}{R_1} > A_1 A_2 C R_2 xy,
\tag{24}
$$

which can be rewritten as

$$
\begin{aligned}
0 &< A_1 C R_1 xy\left(1 - \frac{B_2}{R_1}\right) + A_1 R_1 x + \frac{B_2 R_2 y}{R_1} \\
&= A_1 C R_1 (1 - R_1)\frac{C^*}{C} y\left(1 - \frac{B_2}{R_1}\right) + A_1 R_1 (1 - R_1)\frac{C^*}{C} + \frac{B_2 R_2 y}{R_1} \\
&= Z\left(1 - \frac{C^*}{C}\right) + A_1 \frac{R_2 - R_1}{C},
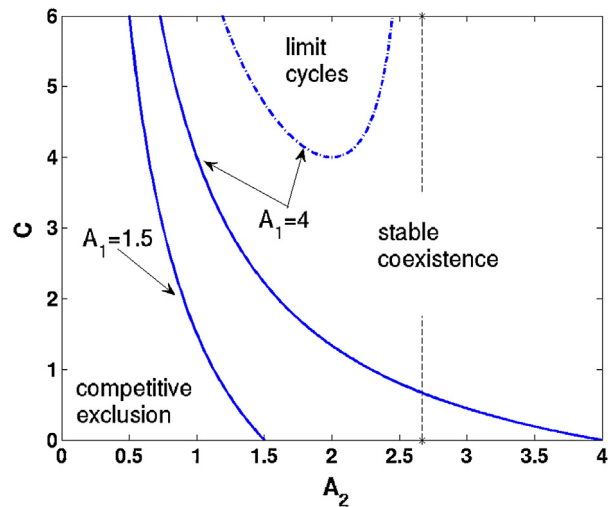\end{aligned}
$$

where

$$
Z = (1 - R_1)\left[A_1\left(1 - \frac{R_1}{R_2}\right)(R_1 - B_2) + B_2\right].
\tag{25}
$$

The stability condition is therefore equivalent to

$$
\begin{aligned}
C &> C^* - \frac{A_1(R_2 - R_1)}{Z} \quad \text{if} \quad Z > 0 \\
C &< C^* - \frac{A_1(R_2 - R_1)}{Z} \quad \text{if} \quad Z < 0.
\end{aligned}
\tag{26}
$$

There are two possible cases. If $Z > 0$, then the coexistence state is stable whenever it exists. When $Z < 0$, then the coexistence state can be destabilized by increasing C sufficiently much above C^*; see

Fig. 4. Coexistence region of both consumers with asymmetric mutualism and predation dynamics. Below the solid curve, where facilitation (C) is weak and catch rate of species y (A_1) is small, species x excludes species y from the system. Above the solid curve, the two can coexist. Above the dash-dot curve, coexistence is unstable. The dashed vertical line gives the threshold of A_2 according to (27). When $A_1 = 1.5$ condition (27) is never satisfied. Death rates B_i are set to unity. Please note that the plot is only relevant where $A_2 < A_1$, by the assumption that x be the better competitor in the absence of facilitation.

Fig. 4. The condition $Z < 0$ is equivalent to

$$A_2 < \frac{B_2}{B_1} \frac{A_1(R_1 - B_2) + B_2}{R_1 - B_2}. \tag{27}$$

In contrast to Fig. 3, this case requires higher values of C for coexistence for higher values of A_1. While the increase in x with A_1 at the semi-trivial equilibrium in the chemostat scenario is linear, this increase is bounded in the logistic scenario. Therefore, a higher value of x cannot necessarily alleviate lower prey levels.

Biological summary: As before, sufficiently strong facilitation from the superior competitor can allow an inferior predator to persist (even if it would not on its own) at a stable coexistence state. Stronger facilitation can destabilize the coexistence state and lead to oscillatory coexistence.

5. Nonlinear predation and facilitation

The linear predation and facilitation functions that we used thus far are not particularly realistic. Predators are satiated at high prey density, which results in bounded predation functions (e.g. Holling II). Likewise, facilitation will eventually level off, so that f_i become bounded functions when there are many consumers. Intuition would suggest that with saturating functions for h_i and f_i, similar effects can be observed as in the linear cases discussed above, except that higher values of C are needed to produce the same dynamic behavior. We confirm this intuition in the case of identical consumers in the chemostat scenario by extending the analysis in Section 3.1.

In addition, a nonlinear functional response can give rise to consumer–resource cycles as in the famous model by Rosenzweig and MacArthur (1963). When we have identical predators in the logistic case (Section 3.2), such consumer–resource cycles occur for a wider range of parameters if there is mutualism.

5.1. Identical consumers in the chemostat scenario

In system (2), we choose monotone, saturating functions for the functional response and the strength of facilitation as

$$h(z) = \frac{az}{1 + qz}, \qquad f(x) = 1 + \frac{\alpha x}{1 + \beta x}. \tag{28}$$

In nondimensional form, the equations read

$$\begin{aligned}
\dot{x} &= x\left(\frac{Az}{1 + Qz}\frac{(1 + (D + C)x)}{1 + Dx} - 1\right), \\
\dot{z} &= 1 - z - \frac{zx}{1 + Qz}\frac{(1 + (D + C)x)}{1 + Dx},
\end{aligned} \tag{29}$$

where $A = az_{in}/d$, $C = \alpha d/(2ae)$, $D = \beta d/(2ae)$, and $Q = qz_{in}$, and the units for x, z, t are the same as in Section 3.1. Parameters D, Q measure how fast the facilitation function and the functional response saturate.

The analysis is similar to the previous case, but the expressions are more cumbersome. It turns out that (a) if $A > 1 + Q$ then the semi-trivial state is unstable; the consumer can invade, and there is a unique positive stable equilibrium; (b) if $A < 1 + Q$, then the semi-trivial state is locally stable; if C is large enough, then the consumer has an Allee effect, i.e. it can persist stably only if it has a high enough initial density. The threshold value for C in the second case is

$$C^* = \frac{1}{A^2}\left[1 + V(AD + 1) + 2\sqrt{V(AD + 1)}\right], \tag{30}$$

where $V = 1 + Q - A$. For $D = Q = 0$, this expression reduces to (6). The effect of Q and D is that when $A < 1 + Q$, higher values of C are required for persistence of the consumer, see Fig. 5.
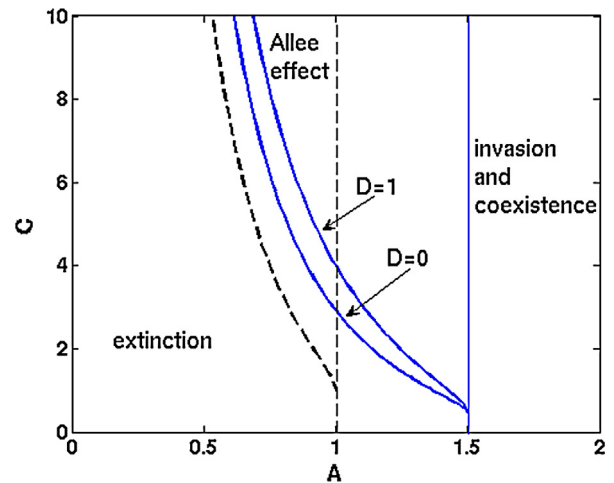

Fig. 5. Illustration of the effect of nonlinear functional response on the dynamics of the mutualism for identical consumers in the chemostat scenario. A Hopf bifurcation occurs at the dashed curve. Higher values of mutualism (C) are required for persistence when D, $Q > 0$ The solid lines have $Q = 0.5$, and $D = 0, 1$ as indicated. The dashed lines are the reference case $Q = D = 0$.

Biological summary: When catch rates saturate, stronger facilitation is required for persistence of the consumer and stable coexistence. As long as the facilitation function is non-decreasing (as we always assume here) the possible dynamics of the two species are qualitatively the same as with linear facilitation and catch rates – but hold for different parameter values.

5.2. Identical consumers in the logistic scenario

The non-dimensionalized system (10) with a type II functional response but linear facilitation function reads

$$\begin{aligned}
\dot{x} &= x\left(\frac{Az(1 + Cx)}{1 + Qz} - B\right), \\
\dot{z} &= z(1 - z) - \frac{xz(1 + Cx)}{1 + Qz},
\end{aligned} \tag{31}$$

where $A = aK/r$, $B = d/r$, $C = \alpha r/(2ea)$, and $Q = qK$. Units of x, z, t are the same as in Section 3.2. For $C = 0$, we obtain the model by Rosenzweig and MacArthur (1963), which has a globally attracting limit cycle, provided $A > (2BQ/(Q - 1)) + BQ$ and $Q > 1$.

The coexistence equilibria satisfy a cubic equation, very similar to the one in (11). As a result, we obtain the following qualitative behaviors. When $A > B(1 + Q)$ then the predator can persist in the system; there is a unique coexistence state. When $A < B(1 + Q)$ then the predator can have an Allee effect if C is large enough. The value of C required for a coexistence state in this case increases with Q (Fig. 6).

The Jacobi matrix at a coexistence state is given by

$$J = \frac{1}{1 + Qz}\begin{bmatrix} ACxz & Bx/z \\ -z(1 + 2C) & z(Q - 1) - 2Qz^2 \end{bmatrix}. \tag{32}$$

Fig. 6 shows that the Hopf bifurcation occurs for smaller and smaller values of A as the strength of facilitation, C, increases. In fact, even very low mutualism reduced the A-value required for limit cycles dramatically.

Biological summary: The classical Rosenzweig–MacArthur model allows for a stable coexistence point or a stable limit cycle, provided the predator has a large enough catch rate. Introducing facilitation into this model has two effects. First, when the catch rate is so small that the predator will die out in the absence of facilitation, then strong enough facilitation can give rise to an Allee effect, as before in Section 3.2. Second, facilitation helps destabilize
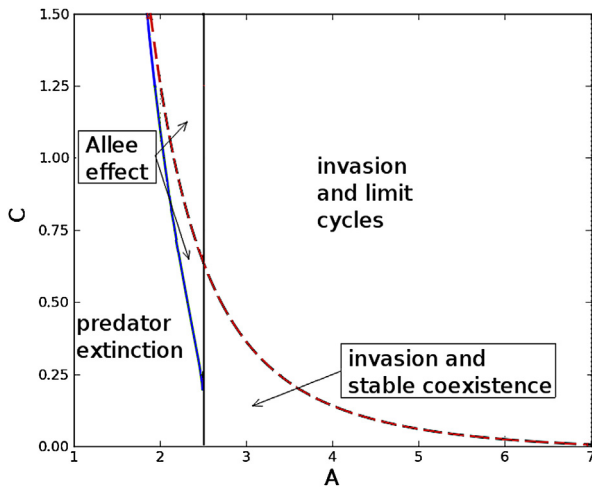
Fig. 6. Illustration of the effect of nonlinear functional response on the dynamics of the mutualism for identical consumers in the logistic scenario. Higher levels of mutualism (C) are required for persistence, yet cycles appear for lower values of C; compare Fig. 2. Parameters values are $B = 1$, $Q = 1.5$. Limit cycles without mutualism appear for $C = 0$ and $A > 7.5$.

the coexistence state and limit cycles can occur for parameter values that would not give limit cycles in the absence of facilitation.

6. The full model

In this section, we combine the results from the two previous simplified cases to infer the dynamics of the full system of intraguild mutualism. We continue to use linear mutualism functions.
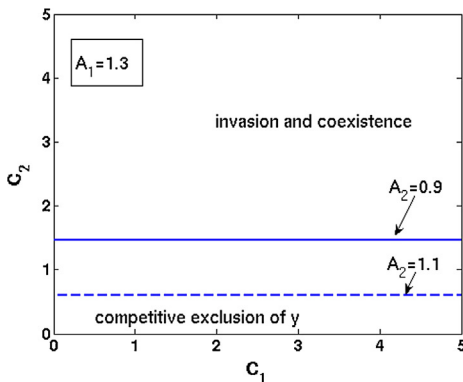
6.1. The chemostat scenario

The nondimensional system with linear functional response and mutualism function reads

$$
\begin{aligned}
\dot{x} &= x[A_1 z(1 + C_1 y) - 1], \\
\dot{y} &= y[A_2 z(1 + C_2 x) - 1], \\
\dot{z} &= 1 - z - z[x(1 + C_1 y) + y(1 + C_2 x)],
\end{aligned}
\tag{33}
$$

where $A_i = a_i z_{in}/d$ and $C_i = \alpha_i d/(a_i e_i)$. The units of x, y, z, t are the same as in Section 4.1. A coexistence state is given by the admissible solution of

$$
A_1 A_2 C_1 C_2 z^2 - (A_1 A_2 C_1 C_2 + A_1 C_2 + A_2 C_1)z + C_1 + C_2 = 0, \tag{34}
$$

so that

$$
x = \frac{1 - A_2 z}{A_2 C_2 z}, \qquad y = \frac{1 - A_1 z}{A_1 C_1 z}, \tag{35}
$$

are positive. At a coexistence state, we also have $z + x/A_1 + y/A_2 = 1$.

Case I: $A_1 > A_2 > 1$

Both semi-trivial steady states exist, and species x can invade species y. In addition, species y can invade species x, leading to coexistence, provided

$$
C_2 > \frac{(A_1/A_2) - 1}{A_1 - 1}, \tag{36}
$$

see Fig. 7, panel (a).

Case II: $A_1 > 1 > A_2$ Only species x can persist by itself. Species y can invade and coexist if (36) is satisfied; see Fig. 7, panel (a).

Case III: $1 > A_1 > A_2$ No semi-trivial states exist. The two species have a 'joint Allee effect', meaning that for large enough C_i, the coexistence state exists and is locally stable. Hence, if mutualism is strong enough and if both species have a high enough initial density, then the two species can coexist; see Fig. 7, panel (b).

We replaced the linear functional responses and mutualism functions with Holling type II functions as in Section 5.1 and explored the qualitative behavior of the system numerically. The results we saw are exactly what one would expect. A type II functional response means a lower catch rate so that higher levels of mutualism are required to obtain coexistence. If mutualism is also modeled by a bounded function, then the required strength may exceed the upper bound. In that case, mutualism cannot be strong enough to allow for coexistence. The effect of nonlinear functional response and facilitation function turns out to be much more interesting in the logistic case, so that we do not pursue it here any further.

Biological summary: There are two cases to consider. If the superior competitor can persist in the absence of facilitation, then the inferior competitor will invade and the two will coexist stably if there is sufficient facilitation from the superior species. If neither of the two species can persist by themselves, then sufficiently strong mutualism can allow both species to coexist stably, provided their initial densities are high enough. The two species exhibit a 'joint Allee effect'. We come back to this case in the discussion; see also Lutscher and Iljon (in press).

6.2. The logistic scenario

The nondimensional system with nonlinear functional response and linear mutualism function reads
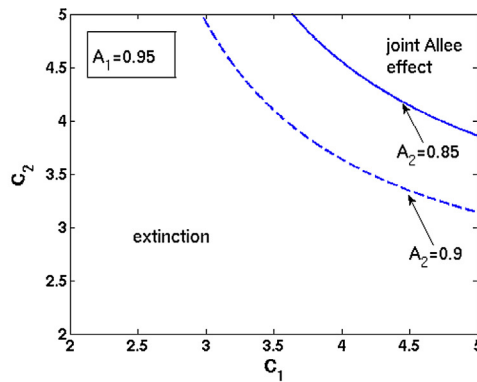
Fig. 7. Coexistence regions in the three-species system with chemostat dynamics with respect to the strength of mutualism of the two species (C_i). Panel (a, left) Catch rates satisfy $A_1 > 1$, $A_1 > A_2$. Species y can invade and the two can coexist if C_2 is large enough. Panel (b, right) $1 > A_1 > A_2$. The two species can coexist if mutualism is high enough and if both have sufficiently high initial density.

$$\dot{x} = x\left[\frac{A_1 z}{1 + Q_1 z}(1 + C_1 y) - B_1\right],$$

$$\dot{y} = y\left[\frac{A_2 z}{1 + Q_2 z}(1 + C_2 x) - B_2\right], \tag{37}$$

$$\dot{z} = z(1 - z) - z\left[\frac{x}{1 + Q_1 z}(1 + C_1 y) + \frac{y}{1 + Q_2 z}(1 + C_2 x)\right],$$

where $A_i = a_i K/r$, $B_i = d_i/r$, $C_i = r\alpha_i/(2e_i a_i)$, and $Q_i = q_i K$. Units of x, y, z, t are the same as in Section 4.2.

When $A_1 > B_1(1 + Q_1)$, then species x can invade the prey-only state $(0, 0, 1)$. The semi-trivial state

$$x = \frac{A_1(A_1 - B_1(1 + Q_1))}{(A_1 - B_1 Q_1)^2}, \qquad y = 0, \qquad z = \frac{B_1}{A_1 - B_1 Q_1} \tag{38}$$

is stable in the x–z plane provided $Q < 1$ or $A_1 < (2B_1 Q_1)/(Q_1 - 1) + B_1 Q_1$; otherwise there is a stable limit cycle; compare Section 5.2. Species y can invade the semi-trivial state if

$$C_2 > \frac{1}{x}\left[\frac{B_2(1 + Q_2 z)}{A_2 z} - 1\right], \tag{39}$$

where x and z are the steady-state values from (38). Similar relationships hold when x and y are exchanged by exchanging indices 1 and 2.

A coexistence state is given by the solution of the cubic equation for species z as

$$z^3 - z^2 + \frac{B_1 B_2(C_1 Q_2 + C_2 Q_1) - A_1 B_2 C_2 - A_2 B_1 C_1}{A_1 A_2 C_1 C_2} z + \frac{B_1 B_2(C_1 + C_2)}{A_1 A_2 C_1 C_2}$$
$$= 0. \tag{40}$$

To find conditions for the existence of a positive solution, we study the equation

$$z^3 - z^2 + \gamma_1 z + \gamma_2 = 0, \qquad \gamma_2 > 0. \tag{41}$$

Local extrema are given by the solutions of

$$3z^2 - 2z + \gamma_1 = 0, \quad \text{i.e.} \quad z_\pm = \frac{1}{6}\left(2 \pm \sqrt{4 - 12\gamma_1}\right). \tag{42}$$

Positive solutions of (40) exist only if the cubic is negative at z_+. When $Q_{1,b}$ are large, then $z_\pm$ are not real, so that no positive solutions of the cubic can exist. When $Q_{1,2}$ are small enough so that z_+ is real (and positive), then the level set

$$z_+^3 - z_+^2 + \gamma_1 z_+ + \gamma_2 = 0 \tag{43}$$

gives the boundary in parameter space between the existence and non-existence of positive solutions for z, and hence the boundary between coexistence and (partial) extinction of all species. Plotting this level set, we found that there are positive solutions for z, provided the mutualism coefficients $C_{1,2}$ are large enough, similar to the chemostat case. Since these plots are qualitatively exactly the same as for the chemostat case, we do not present them here.

Investigating the various cases, we find the exact same qualitative behavior as in the chemostat scenario. Specifically, (i) if species x can invade at low density, then the invasion condition for species y is given by (39), which leads to a qualitative behavior as in Fig. 7, left panel. (ii) if no species can invade at low density and if the coefficients $Q_{1,2}$ are small enough, then there is a joint Allee effect, provided the mutualism coefficients $C_{1,2}$ are large enough (from (40)); see Fig. 8 (left panel). This scenario leads to a qualitative behavior as in Fig. 7, right panel.

In both cases, with or without joint Allee effect, increasing the strength of mutualism can lead to population cycles. If there is no joint Allee effect, all three species will coexist in a limit cycle. If there is a joint Allee effect, then the two predator species could be driven to extinction if cycles become too large; see Fig. 8 (right panel).

Finally, we consider the effect of intraguild mutualism on cyclic coexistence of predators. When $C_{1,2} = 0$, system (37) admits for cyclic coexistence via a transcritical bifurcation of limit cycles as follows. With only one predator, the system is a Rosenzweig–MacArthur system and admits a limit cycle. Under certain conditions, the second predator can invade along the limit cycle, and both can coexist in a limit cycle (Kot, 2001). A necessary condition is that one predator does better at low prey density whereas the other grows faster at high prey density (Hsu et al., 1978). This coexistence mechanism depends on a very fine balance and may occur only in a very narrow interval of parameter values. For example, with $A_1 = 8$, $A_2 = 6$, $B_1 = 1$, $B_2 = 0.8$, and $Q_1 = 3$, the two species coexist in the range of $Q_2 \in [2.63, 2.643]$. Species x does better at low prey density, species y at high density.

Now we add very weak intraguild mutualism of $C_{1,2} = 0.01$. Then the coexistence region along a limit cycle is $Q_2 \in [2.57, 2.704]$, which is much larger than for $C_{1,2} = 0$. Fig. 9 shows such limit cycles and demonstrates that the two predators are in phase with one another. We tested this result for a variety of other parameter combinations, and for all of them we found that the interval of Q_2 that permits coexistence along a limit cycle is larger when weak mutualism is added. In practice, this result means that even if mutualistic effects are relatively small, they may lead to
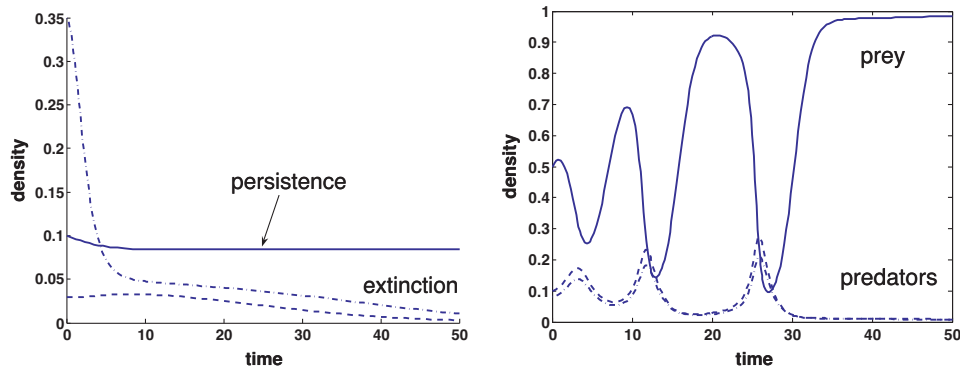
Fig. 8. (Left) Illustrating the joint Allee effect by plotting the density of species y for different initial conditions. When the initial value of species y is too low, it will go to extinction, and species x with it. When $y(0)$ is intermediate, both species can stably coexist. When $y(0)$ is too large, the cyclic nature of consumer–resource dynamics drives species y to low values and from there to extinction. The different initial values are $y(0) = 0.03$ (dashed), $y(0) = 0.1$ (solid), and $y(0) = 0.35$ (dash-dot). Parameter values are $A_1 = 0.95$, $A_2 = 0.85$, $B_1 = 1$, $B_2 = 0.9$, $Q_1 = 0.1$, $Q_2 = 0.05$, $C_1 = 6$, $C_2 = 5$. (Right) Illustrating cycling to extinction when there is no stable coexistence by plotting the density of each species (compare Fig. 2). Parameters are as before, except $Q_2 = 0.1$, $C_1 = 17$, $C_2 = 14$.
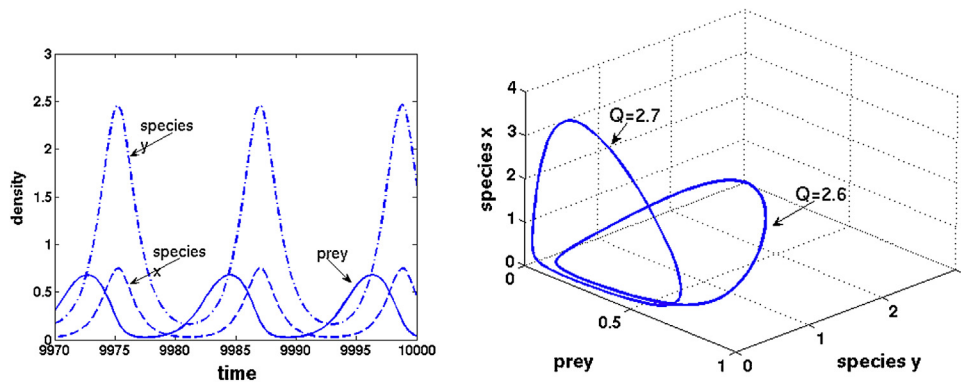
Fig. 9. Cyclic coexistence of two mutualistic predators on one prey. For $Q_2 < 2.57$ there is a stable limit cycle between y and z with $x = 0$. As Q_2 increases, there is a transcritical bifurcation of limit cycles, and the coexistence limit cycle becomes stable. For Q_2 larger than 2.704, the limit cycle between x and z with $y = 0$ is stable against invasion by y. Parameters are $A_1 = 8$, $A_2 = 6$, $B_1 = 1$, $B_2 = 0.8$, and $Q_1 = 3$.

substantially increased likelihood of coexistence between two competing species.

Biological summary: The system with logistic growth of the resource shows the same qualitative behavior as in the chemostat case, and in addition, it supports population cycles. Mutualism can, in fact, destabilize a stable coexistence state. Where coexistence is dependent on population cycles, as in the Rosenzweig–MacArthur model, even low levels of mutualism can enlarge the range of parameters that lead to cycles and to cyclic coexistence.

7. Discussion

Mutualistic interactions between species are well documented empirically but much less studied theoretically than competitive or exploitative interactions (Boucher, 1982; Bruno et al., 2003). Intraguild mutualism in particular could be a mechanism for coexistence between competing species, and could therefore contribute to the creation and maintenance of biological diversity (Stachowicz, 2001). Crowley and Cox (2011) propose a theoretical research program on intraguild mutualism, based on studying several community modules. To our knowledge, this work is the first step in this research program towards understanding causes and effects of intraguild mutualism from a modeling perspective.

Even within each of the modules proposed by Crowley and Cox (2011), one has to make modelling decisions as to which processes are affected by mutualism. Gross (2008) assumed that death rates of competing species decreased in the presence of their

competitors and found stable coexistence between many competitors on a single resource. Alternatively, based on empirical evidence (e.g. Losey and Denno, 1998), we modeled mutualistic interaction by increased feeding rates in the presence of the mutualist. In the first subcase (Section 3), we demonstrated how bistability (Allee effect) can emerge from mutualism. In the second subcase (Section 4), we explored how facilitation can lead to coexistence of consumers and to persistence of consumer that would go extinct on its own. In both cases, the dynamics of the logistic case included cyclic behavior, but not in the chemostat case. Nonlinearities did not introduce new behavior in the chemostat case, but did so in the logistic case, where cycles are present in the absence of mutualism, and mutualism enhances the propensity to cycle (Section 5). In the final section, we put the pieces of the puzzle together and explored some more complex dynamical issues numerically; see Table 1.

One of our results is also that stable coexistence between two intraguild mutualists occurs over a much larger set in parameter space than without mutualistic interactions. Hence, these results by Gross (2008) are robust and independent of the particular mechanism. In addition, we found that mutualism can be a mechanism for destabilization of a stable coexistence state and for emergence of population cycles. This effect only occurred for the logistic scenario. Our results here differ from the results by Gross (2008), who found limit cycles also with linear prey renewal, which corresponds to our chemostat scenario. We speculate that this difference results from the different implementation of mutualism. In our model, enhanced consumption of resources appears in the

Table 1
Summary of models and main results. "Identical consumers" refer to the case in which two consumer species have identical parameter values. h_i denote consumer–resource functional response; f_i are facilitation functions.

Section	Consumers	Scenario	h_i	f_i	Results
3.1	Identical	Chemostat	Linear	Linear	Facilitation extends coexistence region. Allee effect.
3.2	Identical	Logistic	Linear	Linear	Strong facilitation can give large oscillations. Allee effect.
4.1	Different	Chemostat	Linear	Linear	Facilitation promotes coexistence when supporting the inferior competitor.
4.2	Different	Logistic	Linear	Linear	In addition, strong facilitation leads to oscillatory coexistence.
5.1	Identical	Chemostat	Nonlinear	Nonlinear	Stronger levels of facilitation required for coexistence. Allee effect.
5.2	Different	Logistic	Nonlinear	Linear	If facilitation is essential bistability can emerge. When catch rates are large, limit cycles can occur.
6.1	Different	Chemostat	Linear	Linear	When superior competitor persists by itself, facilitation can promote persistence of the inferior competitor. If no competitor persist by itself, then reciprocal or joint Allee effect emerges.
6.2	Different	Logistic	Nonlinear	Linear	In addition, population cycles are possible. Mutualism can destabilize a stable coexistence state.

consumer *and* in the resource equations. In the model by Gross (2008), the mutualistic reduction of death rates appears only in the consumer equation; the effect on the resource is only indirect. Since this effect is only indirect, it could act similarly to a delay, which can easily destabilize a steady state. The third effect that we found is that of a joint Allee effect for the consumer species: neither can persist on the given resource alone, but jointly they can with sufficiently high initial density. A similar effect has recently been found theoretically in a plant–pollinator system (Lutscher and Iljon, in press). We are not aware of empirical evidence for such an effect. However, it is conceivable that so-called 'ecosystem engineers' (Cuddington et al., 2009) would show such effects.

The interaction between an Allee effect (joint or not) and population cycles can lead to a catastrophic collapse of a cyclic population when the cycle becomes so large that it drops below the Allee threshold at its low point. A similar effect was already observed by Conway and Smoller (1986) in a predator–prey system with Allee effect of the prey. Hence, intraguild mutualism can lead to a variety of complex patterns that are otherwise absent from a competitive system.

As part of our analysis, we identified two special cases of parameter regimes that correspond to ecologically relevant situations on their own, namely intraspecific facilitation in a two-species model and uni-directional facilitation in a three-species model. The analysis of these two reduced systems provided crucial understanding of possible patterns in the full systems, yet was much simpler to understand. This observation can help uncover similarities between seemingly quite different ecological scenarios through mathematical scaling.

In addition to cyclic coexistence, systems with competing consumers can also show chaotic dynamics (Abrams et al., 2003). The two predator densities are intermediately correlated in such scenarios. Mutualism tends to synchronize cyclic predator populations; see for example Figs. 8 and 9. This mechanism could be a reason for why we did not see any chaotic dynamics in our simulations, but finding chaos was not our main focus. The question of whether mutualism decreases the likelihood of chaos should be explored in the future.

An important next step in this research is to include spatial movement into the models. We observe that the sign patterns of the Jacobi matrix for the two-dimensional models in Section 3 allows for diffusion-induced instability. Hence, we expect spatial patterns to form when we simply add diffusion terms of sufficiently different magnitude to both species. Our preliminary numerical investigations show that the same is true for the full three-species system (plots not shown), see White and Gilligan (1998) for detailed conditions on Turing patterns in three-species systems. An alternative and much more challenging approach would be to model movement behavior of different intraguild mutualist species where one moves in response to the other as well as the prey. In such a movement model, one could study how higher catch rates in the presence of a competing species might emerge as a result of different (optimal?) foraging strategies.

Acknowledgments

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