

# How predator functional responses and Allee effects in prey affect the paradox of enrichment and population collapses

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## Abstract

In Rosenzweig–MacArthur models of predator–prey dynamics, Allee effects in prey usually destabilize interior equilibria and can suppress or enhance limit cycles typical of the paradox of enrichment. We re-evaluate these conclusions through a complete classification of a wide range of Allee effects in prey and predator's functional response shapes. We show that abrupt and deterministic system collapses not preceded by fluctuating predator–prey dynamics occur for sufficiently steep type III functional responses and strong Allee effects (with unstable lower equilibrium in prey dynamics). This phenomenon arises as type III functional responses greatly reduce cyclic dynamics and strong Allee effects promote deterministic collapses. These collapses occur with decreasing predator mortality and/or increasing susceptibility of the prey to fall below the threshold Allee density (e.g. due to increased carrying capacity or the Allee threshold itself). On the other hand, weak Allee effects (without unstable equilibrium in prey dynamics) enlarge the range of carrying capacities for which the cycles occur if predators exhibit decelerating functional responses. We discuss the results in the light of conservation strategies, eradication of alien species, and successful introduction of biocontrol agents.

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## 1. Introduction

Predator–prey models of the Rosenzweig–MacArthur type (i.e. including logistic growth of the prey and a type II functional and numerical response of the predator) predict destabilization of interior equilibria and the emergence of stable limit cycles with increasing carrying capacity of the environment (Rosenzweig, 1971; Gilpin, 1972). This phenomenon, known as the paradox of enrichment, did not show up in empirical tests with aquatic predator–prey systems (Murdoch et al., 1998; McCauley et al., 1999). Several explanations of this apparent contradiction have

passed theoretical and empirical scrutiny: sigmoidal or other similar non-linear functional responses of the predators (Murdoch, 1969; Oaten and Murdoch, 1975; Hassell and Comins, 1978; Nunney, 1980; Abrams and Roth, 1994; Sugie et al., 1996; Collings, 1997; Oksanen et al., 2001; Gross et al., 2004), mutual interference between predators (Ruxton et al., 1992), hiding of prey (Ruxton, 1995), induction of defenses (Vos et al., 2004; Verschoor et al., 2004), limiting nutrients and more generally the prey quality (Sommer, 1992; Loladze et al., 2000; Andersen et al., 2004), heterogeneity in the prey population with respect to edibility (Abrams and Walters, 1996; Genkai-Kato and Yamamura, 1999; Bohannan and Lenski, 1999; Persson et al., 2001), and patterned distribution in space (Scheffer and De Boer, 1995; Nisbet et al., 1998; Holyoak, 2000; Jansen and de Roos, 2000).

Another mechanism that can prevent predator–prey systems from exhibiting sustained cycles is a (demographic)

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Allee effect, i.e. positive density dependence in prey population growth at low prey densities (Stephens et al., 1999). Strong Allee effects—with negative population growth at low densities—lead to extinction if the population falls below a threshold size or density. If troughs in otherwise plausible prey cycles extend below the Allee threshold density, both prey and predators go extinct. This mechanism has already been shown to lead to a reduced potential for cycles and an increased propensity for system collapse (Courchamp et al., 2000; Kent et al., 2003; Webb, 2003; Zhou et al., 2005).

The Allee effect in prey may be caused by predation or by processes inherent to the prey life history (Dennis, 1989; Sinclair et al., 1998; Stephens et al., 1999; Boukal and Berec, 2002; Liermann and Hilborn, 2001; Gascoigne and Lipcius, 2004). Empirical evidence for Allee effects in single-species animal and plant populations is widespread (Lamont et al., 1993; Hopper and Roush, 1993; Groom, 1998; Kuussaari et al., 1998; Hackney and McGraw, 2001; Morris, 2002; Liebhold and Bascombe, 2003). Some of these observations (e.g. Hackney and McGraw, 2001) in fact point to a weak rather than a strong Allee effect, such that the prey per-capita population growth rate is reduced at low densities but remains positive.

Considerable attention has been given to the role of human exploitation in promoting collapse of animal populations subject to strong Allee effects (e.g. Rowe et al., 2004; Hutchings and Reynolds, 2004) as well as the role of predators (Sinclair et al., 1998; Courchamp and Macdonald, 2001; Gascoigne and Lipcius, 2004; Mooring et al., 2004; Sarnelle and Knapp, 2004). However, theoretical investigations of predator–prey dynamics have only dealt with a limited set of predator functional responses and strong Allee effects (references above). Given that predation is a general ecological mechanism, a more thorough analysis is needed, especially because insights in the role of predation and Allee effects for ecosystem persistence may well be important for population management and species conservation (Sinclair et al., 1998; Courchamp et al., 1999; Gascoigne and Lipcius, 2004).

In this article, we examine how system collapse and limit cycles, characteristic of the paradox of enrichment, are influenced by Allee effects inherent to prey life history on the one hand and the (constant, decelerating or sigmoidal) shape of the predator’s functional response on the other. In particular, we ask to what extent these mechanisms reduce the propensity to exhibit sustained cycles with increasing prey carrying capacity (or decreased predator mortality) in the framework of a Rosenzweig–MacArthur predator–prey model. This is done by bifurcation analysis of this model, extended to include a continuum of functional response shapes and a wider variety of Allee effects than usually considered in other model exercises. This type of analysis has not been carried out before. As we will show, it is critically important to distinguish between weak and strong Allee effects and different types of predator functional responses.

## 2. Model

We base the analysis on a simple model of a predator–prey interaction of the type

$$\frac{dx}{dt} = g(x) - F(x)y,$$

$$\frac{dy}{dt} = -my + eF(x)y, \quad (1)$$

in which  $x$  and  $y$  are the prey and predator densities,  $g(x)$  is the density-dependent prey growth rate,  $m$  is the predator per-capita mortality rate,  $e$  is the predator’s food-to-offspring conversion efficiency, and  $F(x)$  is a laissez-faire type of predator functional response, assuming no interference among individual predators. We use a general representation of the functional response

$$F(x) = \frac{\lambda x^n}{1 + \lambda h x^n} \quad (2)$$

introduced by Real (1977). Parameter  $h$  can be interpreted as the handling time, and  $\lambda$  and  $n$  as scalings of the predator–prey encounter rate. The exponent  $n$  describes the shape of the functional response, yielding decelerating responses for  $0 < n \leq 1$ , including the Holling type II response for  $n = 1$ , and Holling type III (sigmoidal) responses for  $n > 1$ . For  $n \rightarrow 0$ , Eq. (2) approaches a density-independent functional response regarded as a good approximation for certain predatory mites (van Baalen and Sabelis, 1995). A plausible mechanistic explanation for integer values of  $n$  involves the Holling disk equation with the prey encounter rate equal to  $\lambda x^n$ , in which  $n$  can be related to the number of encounters a predator must have with the prey before becoming maximally efficient (Real, 1977). For  $0 < n \leq 1$ , per-capita predation rates of the prey are higher at low prey densities, i.e. predation alone leads to a component Allee effect in the sense of Stephens et al. (1999) if the feedback through changing predator densities is disregarded.

We further assume that the prey exhibits a demographic Allee effect at low population densities due to reasons other than predation by the focal predator. The equation describing the prey dynamics can be interpreted, for example, as a heuristic approximation of a two-sex population dynamics where the differences between the sexes are not explicitly modelled (Dennis, 1989), or as an impact of another, generalist predator with a Holling type II functional response (Gascoigne and Lipcius, 2004). Alternatively, it can be seen as an approximation of group dynamics under obligate cooperation (Courchamp et al., 2000).

Given these assumptions, Eq. (1) becomes

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) \left(1 - \frac{A+c}{x+c}\right) - \frac{\lambda x^n}{1 + \lambda h x^n} y,$$

$$\frac{dy}{dt} = -my + \frac{\lambda x^n}{1 + \lambda h x^n} y, \quad (3)$$

where  $r$  scales the prey growth rate,  $K$  is its intrinsic carrying capacity,  $A$  is the Allee threshold, and  $c$  is an auxiliary parameter ( $c > 0$  and  $A \geq -c$ , Boukal and Berec, 2002). The auxiliary parameter  $c$  affects the overall shape of the per-capita growth curve of the prey. As  $c$  increases, the curve becomes increasingly “flatter” and reaches lower maximum values (Fig. 1). Predator’s conversion efficiency  $e$  has been scaled away from Eq. (3) by a simple linear transformation ( $\tilde{t} = et$ ,  $\tilde{y} = y/e$ ,  $\tilde{r} = r/e$ ,  $\tilde{m} = m/e$ , tildes dropped). Only a part of the functional response eventually plays a role in the dynamics given that viable prey populations become constrained between  $A$  and  $K$ ; the shape of the functional response in that range is discussed in more detail in Appendix A.

The Allee effect is strong if  $A > 0$ : the prey exhibits two non-zero equilibria in the absence of predators and goes extinct below the Allee threshold (Fig. 1). For  $A < 0$ , the Allee effect is weak: the lower unstable equilibrium disappears and the origin becomes unstable. For  $A > -cK/(c + K)$  the prey population exhibits a demographic Allee effect in the sense of Stephens et al. (1999), i.e. the prey per-capita growth rate is positively density dependent at low densities. For smaller  $A$ , the prey per-capita growth rate becomes negatively density dependent for all population densities. Eq. (3) is the standard Rosenzweig–MacArthur model for the limiting case  $A = -c$  and  $n = 1$ .

Eq. (3) has three boundary equilibria:  $E_0 = (0, 0)$ ,  $E_u = (A, 0)$  and  $E_s = (K, 0)$ , of which  $E_0$  and  $E_s$  are locally stable and  $E_u$  locally unstable in the prey-only subspace. For a finite range of the predator mortality rate  $m$  (Appendix B), Eq. (3) has a unique interior equilibrium

$$E^* = (x^*, y^*) = \left( F^{-1}(m), \frac{g(F^{-1}(m))}{m} \right) \tag{4}$$

in which the prey equilibrium density equals

$$x^* = F^{-1}(m) = \left( \frac{m}{\lambda(1 - hm)} \right)^{1/n} \tag{5}$$

$E^*$  thus requires  $hm < 1$  to exist.

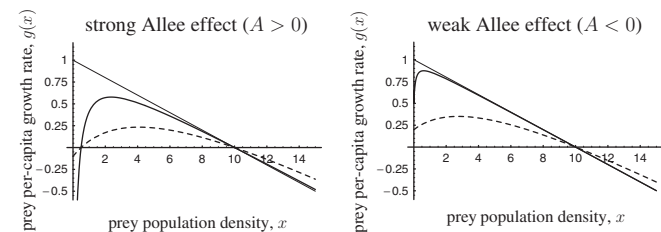


Fig. 1. Per-capita growth rate of the prey in (3) in the absence of predators. Parameter values:  $r = 1$ ,  $K = 10$ . Left panel:  $A = 0.5$ ,  $c = 0.1$  (thick curve);  $A = 0.5$ ,  $c = 5$  (thick dashed curve). Right panel:  $A = -0.05$ ,  $c = 0.1$  (thick curve);  $A = -1$ ,  $c = 5$  (thick dashed curve). Thin line in both panels indicates the limiting case of logistic growth.

### 3. Results

The standard Rosenzweig–MacArthur model exhibits three types of behavior (Křivan, 1996): predator extinction for  $K \leq m/\lambda(1 - hm)$ , which also follows from (7) with  $n = 1$  (see Appendix B); stationary coexistence at  $E^*$  for  $m/\lambda(1 - hm) < K \leq (1 + hm)/\lambda h(1 - hm)$ ; and a stable limit cycle surrounding an unstable equilibrium  $E^*$  for  $K > (1 + hm)/\lambda h(1 - hm)$ .

#### 3.1. Local stability analysis

We first extend this result by deriving general stability conditions for the interior equilibrium  $E^*$ . Table 1 lists all possible configurations of the predator and prey isoclines and corresponding dynamics. Given the laissez-faire type of the functional response and the lack of any other density-dependent processes in the predator population, the predator isocline in Eq. (3) is a vertical line at the equilibrium prey density  $x^*$ . The prey isocline is a hump-shaped function of the prey density, positive only for  $x \in (A, K)$  (for  $x \in (0, K)$  if  $A < 0$ ). It has one or two (local) maxima and zero or one local minimum in that interval. The determinant of the Jacobian matrix associated with (3) is always positive in  $E^*$  (Appendix C), and  $E^*$  is therefore stable if the prey isocline has a negative slope at  $E^*$  and unstable if the slope is positive.

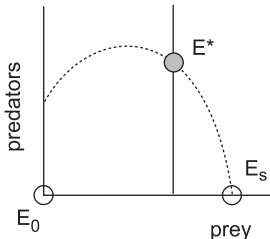
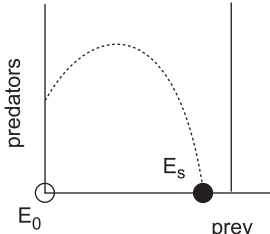
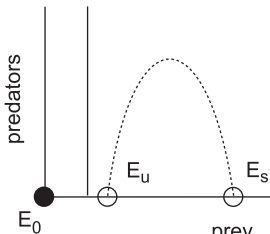
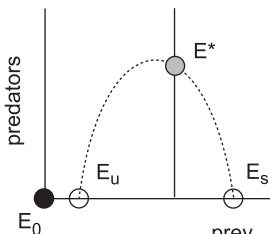
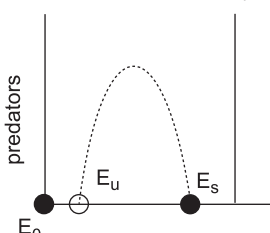
If the prey isocline has a single maximum,  $E^*$  can change stability only once from stable to unstable as  $K$  increases or  $m$  decreases. If the isocline has two maxima and one minimum,  $E^*$  can change stability three times (stable  $\rightarrow$  unstable  $\rightarrow$  stable  $\rightarrow$  unstable as  $K$  increases or  $m$  decreases). The prey isocline may also have one maximum and one minimum if the Allee effect is weak or absent, such that  $E^*$  changes from stable to unstable to stable. Moreover, the maximum (or both maxima) of the prey isocline shifts to higher prey densities as the strength of the Allee effect given by  $A$  increases while the vertical predator isocline remains in the same position, thereby enlarging the interval of  $K$  in which the interior equilibrium  $E^*$  can become unstable.

Inequalities (11)–(14) derived in Appendix C provide general analytic conditions for the local stability of  $E^*$ . For a prey with logistic growth ( $A = -c$ ), the paradox of enrichment can occur if and only if  $n < (1 - hm)^{-1}$  and thus becomes less feasible (e.g. the range of  $m$  leading to the paradox of enrichment decreases) when the functional response becomes more sigmoidal (exponent  $n$  increases). Moreover, the interior equilibrium  $E^*$  remains stable for any  $K$  and strong Allee effects with small but positive  $A$  if  $c$  and  $m$  are sufficiently small and  $n$  is sufficiently large (compare the predator with Holling type III functional response in the right panel of Fig. 3B).

#### 3.2. Bifurcation analysis

To obtain a complete classification of the qualitative behavior of model (3), we analyze the bifurcation pattern in

Table 1  
Five major types of isocline configuration and corresponding dynamics of model (3)

Isoclines	Dynamics (areas in Fig. 3)
<p>Case 1</p> 	<p>Stable coexistence/cycles (Stable Equilibrium, Locally Stable Equilibrium, Paradox of Enrichment Cycles, Stable Equilibrium/PoE Cycles)</p>
<p>Case 2</p> 	<p>Prey-only; predator cannot establish (Prey Only)</p>
<p>Case 3</p> 	<p>Collapse (Extinction 2)</p>
<p>Case 4</p> 	<p>Collapse or stable coexistence/cycles (Extinction 1, Stable Equilibrium, Locally Stable Equilibrium, Paradox of Enrichment Cycles, Stable Equilibrium/PoE Cycles)</p>
<p>Case 5</p> 	<p>Collapse or prey-only; predator cannot establish (Prey Only)</p>

Dotted curve = prey isocline (diagrammatic; the isocline can have one or two peaks; equilibrium  $E^*$  can be to the left or right of either isocline peak); solid line = predator isocline. Equilibria (see text for notation): black = always stable; transparent = always unstable; gray = stable or unstable.

the XPPAUT package (Ermentrout, 2002), and illustrate the results with two values of  $c$ . The classification requires up to five codimension-one bifurcations: branching points corresponding to predator invasion, “simple extinction” branching points corresponding to the (dis)appearance of the interior equilibrium  $E^*$  and unconditional collapse of the predator–prey system, Hopf bifurcation points in which  $E^*$  exchanges stability, limit points of cycles in which a stable and an unstable cycle collide, and

bifurcation points tracking a heteroclinic orbit leading from the prey-only stable equilibrium  $E_s$  to the prey-only unstable equilibrium  $E_u$ . There are up to six bifurcation branches for any given two-parametric projection: one heteroclinic branch, two branches of Hopf bifurcation points given by (12), one branch of predator invasion points given by (7), one branch of limit points of cycles, and one branch of simple extinction points given by (8), all with inequalities replaced by equalities (Appendix B).

The simple extinction branch is absent if  $A \leq 0$ , the heteroclinic branch is absent if  $A > 0$ , and the limit points of cycles do not occur if  $K$ ,  $c$  or  $n$  are sufficiently low.

Four of the six bifurcation branches are rooted in a single point  $m_r = \lambda / (1 + \lambda h)$  as  $n \rightarrow 0$  in the projection to the  $(m, n)$  parameter plane (Figs. 2 and 3A), and in the point  $A_r = K_r$  with  $m_r$  (Fig. 3B) or  $K_r$  (Fig. 3C) given by (7) in projections with  $n > 0$  (see Appendix D for more details). One of the Hopf branches (as well as the branch of limit points of cycles) does not reach the common point. It is the branch approaching  $m = 0$  as  $n \rightarrow \infty$  if both  $K$  and  $c$  are large enough (left panel in Fig. 3A), and the branch approaching  $m = 1/h$  as  $n \rightarrow \infty$  if  $K$  or  $c$  is small (right panel in Fig. 3A).

The branches delimit seven major parameter domains in which the interior equilibrium exists or does not exist, is stable or unstable, and is or is not surrounded by a stable or an unstable limit cycle or by both. We show all these domains in Fig. 3A, which focuses on the predator’s life history—its mortality rate  $m$  and the shape of the functional response embodied in the exponent  $n$ . The other four panels in Fig. 3 target the prey life history ( $K$  and  $A$ , Fig. 3B) and an interplay of the Allee effect in prey and predator mortality ( $A$  and  $m$ , Fig. 3C).

In Extinction 1 and 2 domains, the system collapses for any initial conditions that involve predators. There is no interior equilibrium in Extinction 2 (Case 3 in Table 1), while an unstable source exists in Extinction 1 (Case 4). In Prey-Only domain, predators cannot establish (i.e. cannot initially increase in density after being introduced in a very

small quantity into the prey-only equilibrium  $E_s$ ; Cases 2 and 5). In the domain of Locally Stable Equilibrium, initial conditions inside an unstable limit cycle lead to the locally stable equilibrium  $E^*$  while those outside the cycle result in ever-increasing oscillations and, if  $A > 0$ , in a deterministic collapse (Cases 1 and 4). A small inoculum of predators introduced into the prey-only equilibrium  $E_s$  thus drives the system to collapse if  $A > 0$ . In domains denoted as Paradox of Enrichment Cycles (PoE Cycles) and Stable Equilibrium, both populations coexist after introducing a small inoculum of predators (Cases 1 and 4). In Stable Equilibrium domain, population densities reach the equilibrium  $E^*$  while populations in the PoE Cycles domain reach the well-known cycles of the paradox of enrichment (Rosenzweig, 1971; Gilpin, 1972). Equilibrium  $E^*$  can be stable and surrounded by an unstable and a stable cycle if  $K$ ,  $c$  and  $n$  are all sufficiently large (Stable Equilibrium/PoE Cycles domain, Cases 1 and 4).

Overall, predators with type III functional responses and sufficiently low mortality rates induce cycles for a much smaller range of Allee effects and prey carrying capacities as compared to the Holling type II response (dashed vs. solid lines in Fig. 3B and C). Appendix D further shows and Fig. 3A illustrates that the Hopf point branch (thick black curve) rooted in the common point  $(m_r, 0)$  in the  $(m, n)$  plane “moves to the left” with decreasing  $c$ . However, the heteroclinic branch (thick gray curve) changes less, thereby leading to a much smaller PoE domain as  $c$  decreases. For  $c = 0.1$  (Fig. 3A, right panel), the PoE domain for  $n < 2$  almost disappears; recall that  $c$

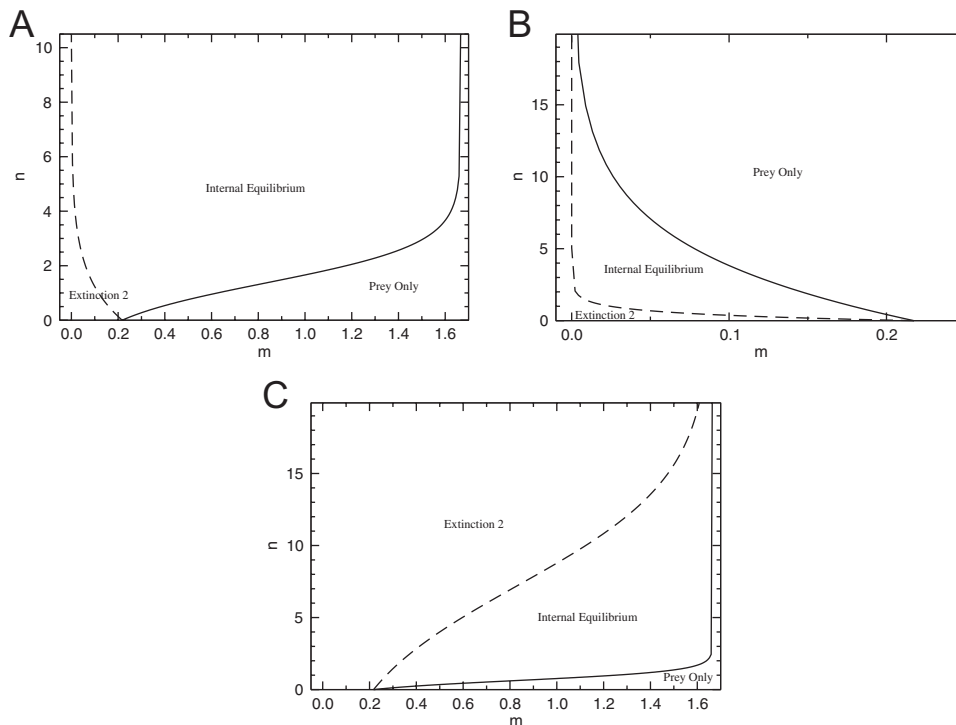


Fig. 2. Three generic cases showing the region of existence of the interior equilibrium  $E^*$  in relation to predator mortality ( $m$ ) and shape of the functional response ( $n$ ). Solid and dotted curves given by inequalities (7) and (8) in Appendix B, respectively.

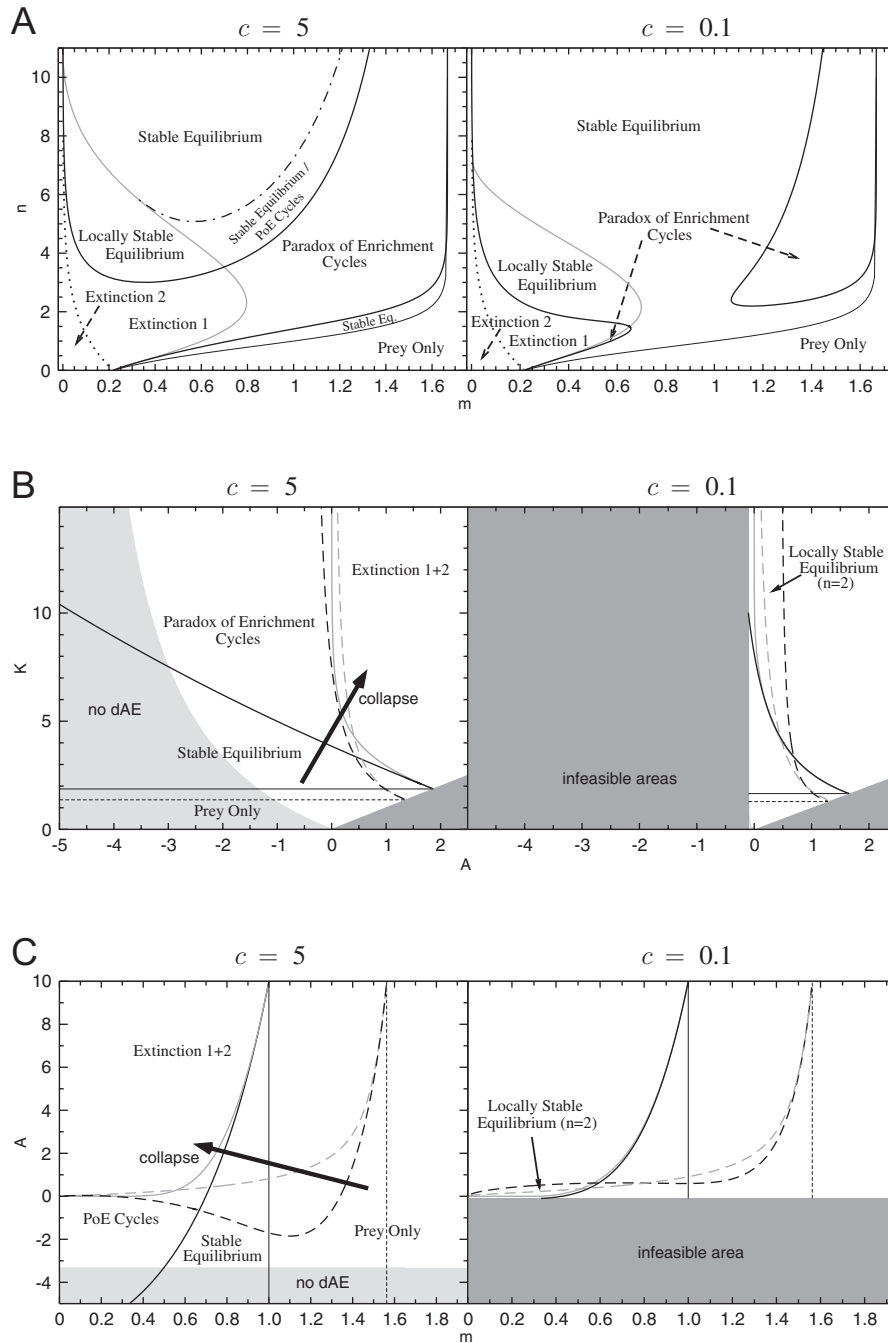


Fig. 3. Bifurcation diagrams of model (3) for  $r = 1$ ,  $\lambda = 0.25$ ,  $h = 0.6$ . Left column:  $c = 5$ , right column:  $c = 0.1$ . Thick arrows illustrate possible routes to a deterministic collapse of the system. Thick gray solid/dashed curves = branches of heteroclinic orbits; thick black solid/dashed curves = branches of Hopf points given by (12); thin black solid/dashed curves = predator invasion curves given by (7); dot-dashed curve = branch of limit points of cycles; dotted curve = simple extinction curve given by (8), omitted in (B) and (C). (A)  $K = 10$ ,  $A = 0.5$ . (B)  $m = 0.365$  (left panel) and  $m = 0.331$  (right panel). Dark gray areas = infeasible areas ( $A \geq K$  or  $A \leq c$ ); light gray areas = no demographic Allee effect (no dAE). Solid curves = Holling type II functional response ( $n = 1$ ), dashed curves = Holling type III functional response ( $n = 2$ ). (C)  $K = 10$ . Lines and areas as in (B); area of no demographic Allee effect negligible for  $c = 0.1$ .

characterizes the overall shape of the prey per-capita growth rate (Fig. 1). In more extreme cases, illustrated by  $c = 0.1$  and  $n = 2$ , the position of the Hopf point branch and the heteroclinic branch reverse for a wide range of other parameter values such that sustained cycles become impossible (dashed lines in right panels of Fig. 3B and C).

The analysis highlights two major routes by which paradox of enrichment and population collapses can arise. Both routes require a decline in the predator mortality rate or increase in the carrying capacity of the prey (Rosenzweig, 1971; Gilpin, 1972) or increase in the severity of the Allee effect (arrows in Fig. 3). We illustrate them by

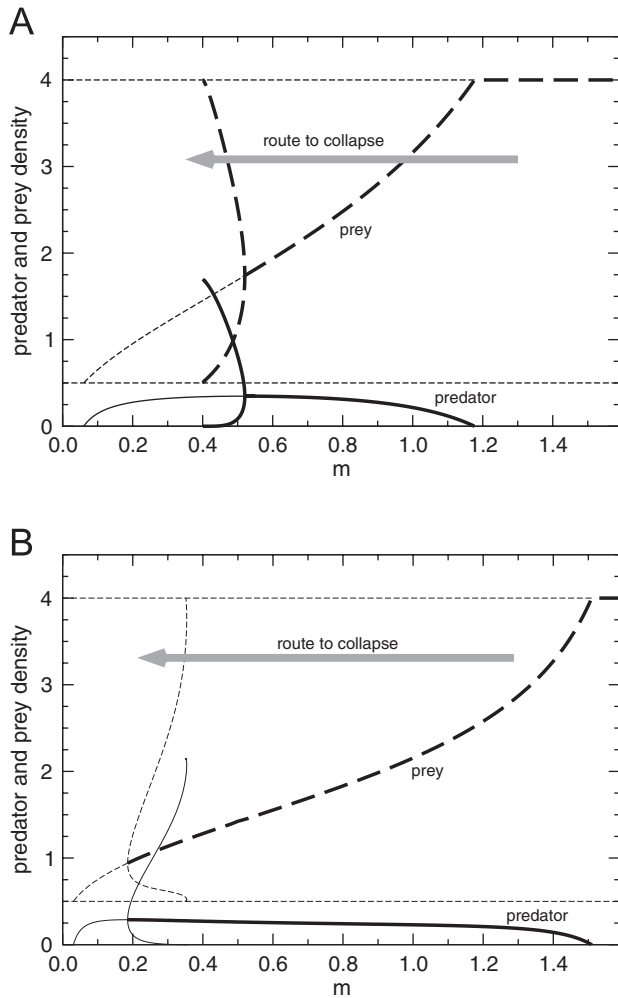


Fig. 4. Bifurcation diagrams showing two different routes to collapse under strong Allee effects. Dashed lines = prey densities; solid lines = predator densities; thick and thin lines = stable and unstable equilibria/cycles, respectively; horizontal lines = prey-only equilibria; limit cycles shown as maximum and minimum values; equilibrium  $E^0$  (locally or globally stable for all  $m$ ) not shown. (A) First route via supercritical bifurcation of the interior equilibrium and subsequent collapse of the stable limit cycle. Model (3) with  $r = 1$ ,  $K = 10$ ,  $A = 0.5$ ,  $c = 5$ ,  $\lambda = 0.25$ ,  $h = 0.6$ , and  $n = 2$ . (B) Second route via subcritical bifurcation, i.e. disappearance of the unstable limit cycle surrounding the interior equilibrium. Same parameter values except  $n = 3$ .

a decreasing predator mortality rate (Fig. 4). The behavior of the system is initially the same as in the absence of the (strong) Allee effect: predators can establish once their mortality rate decreases below a threshold (Rosenzweig, 1971; Gilpin, 1972). However, the system eventually collapses at low but positive predator mortality rates if the Allee effect is strong. In the first route for low exponents  $n$ , equilibrium  $E^*$  loses stability via a supercritical Hopf bifurcation and, before the collapse via a heteroclinic bifurcation, gives rise to stable limit cycles as in the “standard” case of the paradox of enrichment (Fig. 4A). This route was included by Webb (2003) among possible scenarios for evolutionary suicide. In the other route for sufficiently high  $n$ , equilibrium  $E^*$  retains its

stability but becomes surrounded by an unstable limit cycle, such that trajectories starting close to the Prey-Only equilibrium  $E_s$  no longer approach  $E^*$  but the origin. At sufficiently low predator mortality rates, the unstable limit cycle disappears in a subcritical Hopf bifurcation before the system collapses (Fig. 4B). These differences arise from changes in the mutual position of the Hopf and heteroclinic bifurcation curves (Fig. 3A).

#### 4. Discussion

Our analysis re-emphasizes the original idea of Rosenzweig (1971) that enrichment of the environment can lead to a collapse of the entire predator–prey system via increasing oscillations. Rosenzweig considered the extinction in a stochastic sense. More recent studies showed that the extinction becomes more acute, i.e. deterministic and abrupt, if the prey exhibits a strong Allee effect (Courchamp et al., 2000; Kent et al., 2003; Webb, 2003; Zhou et al., 2005). When conditions are met for the predator–prey system to cycle, the prey population in the trough of the cycle is not only subject to stochasticity but also to a strong Allee effect in growth, and this makes both populations prone to extinction. Most likely, any other mechanism causing the populations to cycle would lead to the same outcome.

In this paper, we analyzed a wide range of Allee effects and predator functional responses to see how they affect the propensity of predator–prey systems to oscillate and/or collapse. Our results thus provide a full classification of possible dynamics and in turn provide several important messages for applications.

Overall, we found that although the exact shape of functional response is of limited importance to the global bifurcation patterns—in agreement with Collings (1997) who analyzed a predator–prey system of the Leslie–Gower type—, its sigmoidal property does matter. For strong Allee effects ( $A > 0$ ), increasingly more sigmoidal functional response can enlarge the area in which the interior equilibrium exists (Fig. 2A), compromise the predator’s ability to establish (Fig. 2B), or strengthen its ability to drive the system to a collapse (Fig. 2C). The three different qualitative impacts are related to which part of the functional response (accelerating vs. decelerating) is highlighted by the “focal” range of prey densities ( $A, K$ ).

##### 4.1. System collapses: the importance of functional response

The ability of predators to locate prey at low prey densities is crucial for system collapses and the paradox of enrichment in Rosenzweig–MacArthur models. Type III functional responses can create a temporary refuge for the prey when at low densities and stabilize the interior predator–prey equilibrium (e.g. Oaten and Murdoch, 1975). Other mechanisms, such as the existence of small spatial refuges for the prey, can have the same effect. The severity of the (strong) Allee effect and predation pressure

then determine whether the system collapses (Fig. 3C). Even for potentially high predation pressure, e.g. due to very low predator mortality, the prey may avoid deterministic extinction if the refuge range extends above the Allee threshold (high  $n$  in Fig. 3A).

As a consequence of this stabilization property, the collapse of the predator–prey system comes unannounced for a broad range of type III functional responses. The impending extinction is only signalled by decreasing prey equilibrium densities and can occur well above the Allee threshold (Fig. 4B). This type of dynamics thus does not yield any qualitative early warning signals—such as the paradox of enrichment—that could be used e.g. in conservation strategies. This phenomenon has not been mentioned in previous models focused on the role of the Allee effect in predator–prey interactions (Courchamp et al., 2000; Kent et al., 2003; Webb, 2003; Zhou et al., 2005).

#### 4.2. Paradox of enrichment: the importance of weak Allee effects

Counterintuitively, we have also found that model (3) can actually exhibit a higher propensity towards the paradox of enrichment under the Allee effect. This is another new result not covered by previous theoretical studies on the subject. The populations can cycle for a larger range of prey carrying capacities and predator mortality rates when the Allee effect is weak and predators have type II or weakly sigmoidal functional responses (Figs. 3B and C). The paradox of enrichment is promoted by flat-shaped prey per-capita growth rates (e.g. by increasing parameter  $c$ , Fig. 1). We are not aware of any experimental or observational data that would allow assessing the impact of the Allee effect on the overall shape of the population growth rate. Our analyses therefore highlight the need to consider such phenomena.

#### 4.3. Perspectives for species conservation, pest management, and biological control

The key assumptions and components of model (3) have received some empirical support and it is therefore worth to point out potential consequences of our theoretical results for population processes in more detail. Below, we consider three areas of applied population biology to illustrate what role the insights gleaned from our analysis may play in population management.

First, commercial exploitation or habitat loss may bring populations at and beyond the brink of extinction. Many proximate mechanisms might be involved in the extinction of small populations (inbreeding, demographic stochasticity, etc.) but Allee effects are at least suspected to rank high on the list. Examples of formerly abundant population, most likely suffering from a strong Allee effect at low densities, include the Atlantic cod and top predatory fish in general (de Roos and Persson, 2002; Rowe et al., 2004;

Hutchings and Reynolds, 2004), the African wild dog (Courchamp and Macdonald, 2001; Courchamp et al., 2002), and the desert bighorn sheep (Mooring et al., 2004). One possible counter-measure to save small groups of an endangered species is to cull its predators (Sinclair et al., 1998; Courchamp et al., 2002; Mooring et al., 2004). This is where our model can have an important message: this activity should take into account predators' efficiencies to locate and/or attack prey at densities close to the Allee threshold. Culling predators with negligible predation pressure at such low densities, e.g. due to a type III functional response or the existence of prey refuges, may (initially) have little effect on the prey growth (Fig. 5A). On the other hand, culling predators with type II functional response but otherwise identical predator and prey life histories might save the prey from extinction (Fig. 5B). Our results emphasize the need for this kind of detailed information on predator functional responses (Sinclair et al., 1998). Obviously, other direct and indirect food web interactions, such as multiple predators sharing the prey, should be carefully examined in studies aiming at specific predator–prey systems.

Second, invasions of alien species (exotics or genetically manipulated organisms) represent a risk of considerable economic concern. Appropriate measures can reduce the risk of such invasions but cannot fully exclude them. Thus, we need to develop strategies to combat successful invaders. Liebhold and Bascompte (2003) make the important point that contrary to the commonly held belief, eradication can be achieved by less than 100% removal of the alien species if it suffers from a strong Allee effect. Using a historical data set of the invasion dynamics of small isolated populations of the gypsy moth, they showed that 80% removal can be sufficient in small populations. Such mortality levels are still high but may be achieved by environmentally safe pesticides or by the collective action of introduced or natural enemies (Dwyer et al., 2004; Ferguson et al., 1994; Elkinton et al., 2004). In the example in Fig. 4B, predators with mortality rate below  $m \sim 0.18$  reduce the equilibrium prey density by  $\sim 80\%$  and the Allee effect subsequently secures full eradication of the pest.

To drive pest populations subject to a strong Allee effect to extinction, natural enemies should be released when pest population density is still sufficiently low or they should be efficient and/or abundant enough to bring the pest population below the Allee threshold. If the pest population is well above the threshold and the enemies are rare, a pest outbreak may be unavoidable before the pest drops below the threshold density and collapses. Analysis of model (3) stresses that in any case the natural enemies should be efficient at low pest densities. This excludes some predators and parasitoids with steep type III functional responses, i.e. high  $n$ , which cannot reach the pest in some refuges. On the other hand, any pest life history (i.e.  $r$ ,  $K$ ,  $A$ , and  $c$ ) is associated with an “optimal” shape of the functional response (exponent  $n$  between  $\sim 1$  and  $\sim 2$  in our

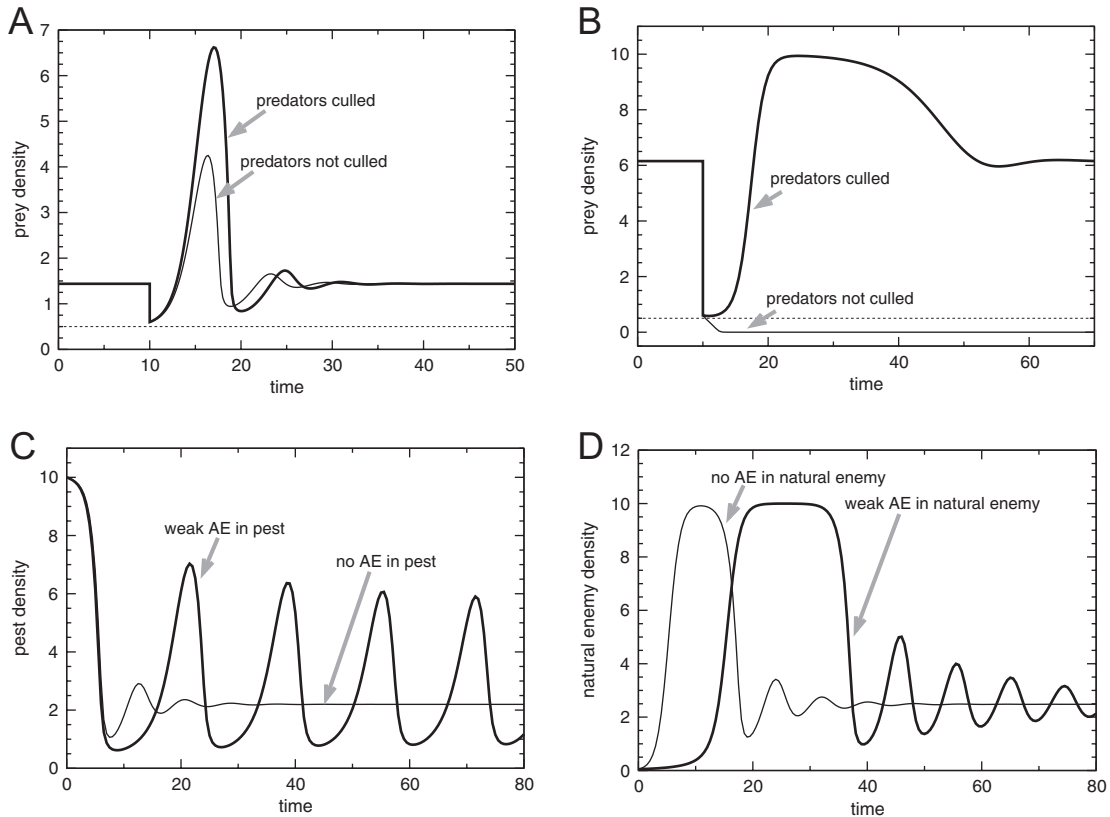


Fig. 5. Population dynamics of the prey in model (3). (A) Recovery after a sudden population crash from equilibrium ( $t = 10$ ) when their only predator with type III functional response is culled at  $t = 10$  to 33% of its population size (thick line) or not (thin line). Allee threshold indicated by a dashed line. (B) Same as (A) but with type II functional response of the predator. (C) The effect of introducing a small number of predators when the pest (= prey) exhibits no Allee effect (thin line) or a weak Allee effect (thick line). (D) The effect of top predators on a released natural enemy (= prey) with no Allee effect (thin line) and with a weak Allee effect (thick line). Parameter values:  $r = 1$ ,  $K = 10$ ,  $\lambda = 0.25$ ,  $h = 0.6$  ((A)–(D));  $A = 0.5$ ,  $c = 0.1$ ,  $m = 0.8$ ,  $n = 1$  (A);  $A = 0.5$ ,  $c = 0.1$ ,  $m = 0.8$ ,  $n = 1$  (B);  $A = -5$  (thin line) and  $-0.5$  (thick line),  $c = 5$ ,  $m = 0.7$ ,  $n = 2$ ,  $x(0) = 10$ ,  $y(0) = 0.01$  (C);  $A = -1$  (thin line) and  $-0.1$  (thick line),  $c = 1$ ,  $m = 0.8$ ,  $n = 2$ ,  $x(0) = 0.05$ ,  $y(0) = 0.01$  (D).

analyses) for which the range of predator mortalities leading to pest eradication is largest (Fig. 3A).

The analysis further shows that pest populations can exhibit higher propensity for sustained cycles under a weak Allee effect when exposed to enemies with an appropriate functional response and mortality rate (Fig. 5C). In the troughs of these cycles, the pest population grows at substantially reduced rates but the peaks of the cycles may actually represent repeated pest outbreaks. Thus, inducing weak Allee effects, e.g. through partial disruption of mating opportunities, along with the introduction of natural enemies may give rise to a desirable reduction in pest abundance in the short run but not prevent outbreaks in the long run.

Third, successful biological control does not only depend on the traits of the natural enemies but also on the quantities released. In some cases, mass rearing is so efficient that large numbers can be introduced in a given area (inundative releases) and for their short-term impact, it is the functional (not the numerical) response that matters. However, mass rearing is usually not so efficient or is not (economically) feasible. In that case, the enemies are released in small numbers (inoculative releases) and

they should have a strong functional and numerical response to increasing pest densities. Such inoculative releases are definitely not always successful. Among the many and varied explanations, Hopper and Roush (1993) proposed—after analyzing a large data set on biocontrol attempts—that failures may be due to poor mate finding chances among the enemies released. Although in need of further investigation, it is a fact that biocontrol workers repeatedly rank the possibility of the mate-finding Allee effect high on their list of possible causes for failure of inoculative enemy releases (Hopper and Roush, 1993; M.W. Sabelis, unpublished data). An awareness is also growing that the enemies released do not only interact with the target pest but become an integral part of the local ecosystem including intraguild predators and hyperpredators.

Thus, we take here our results one step further and consider that the released predator becomes a potential prey of another top predator, and drop the dynamics of the basal prey. For example, failures to control waterlettuce by caterpillars of the moth *Spodoptera pectinicornis* in Florida (USA) were attributed to boat-tailed grackles, fire ants, and spiders (Dray et al., 2001). The latter may predate

upon the enemy inoculum much like we have supposed in model (3). The released enemies may be driven to extinction by their enemies, e.g. due to strong Allee effects, or remain rare and little effective initially, yet become more effective later in time. In view of the latter phenomenon, biocontrol workers often decide to look for alternative enemies or suppose that the natural enemy needs to gradually adapt to its new environment (M.W. Sabelis, unpublished data). However, analysis of model (3) hints at an alternative explanation: the change in effectiveness can be due to a weak Allee effect in the growth rate of the released enemy (Fig. 5D). A tri-trophic model is needed to investigate fully this alternative explanation but is beyond the scope of this paper. Such a model could also incorporate Allee-like phenomena which arise through nutritional constraints for herbivores in autotroph–herbivore–carnivore systems (Loladze et al., 2000; Andersen et al., 2004); we have not explicitly considered such mechanisms here.

As a final take-home message, we would like to emphasize that such alternative explanations are the prime asset of our and similar model exercises. For this reason, feedback from theoretical models provides useful guidelines for practitioners in biological control and other fields of applied population biology.

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**Appendix A. Properties of the functional response**

The functional response (2) is decelerating for all prey densities for  $0 < n \leq 1$  and becomes increasingly sigmoidal if  $n > 1$ . The inflection point  $x_i(n)$  of the sigmoidal functional response can be found by differentiating (2) twice with respect to  $x$  and setting the resulting expression equal to 0, which yields

$$x_i(n) = \left( \frac{n-1}{\lambda h(n+1)} \right)^{1/n}. \tag{6}$$

A straightforward analysis of (6) shows that for  $n \in (1, +\infty)$ ,  $x_i(n)$  increases monotonically from 0 to 1 if  $\lambda h \geq 1$  but becomes hump-shaped if  $\lambda h < 1$ , increasing initially from 0 above 1 and subsequently decreasing asymptotically to 1. The hump is steeper and higher as  $\lambda h$  decreases. The shape of the functional response in the focal range of prey densities— $(A, K)$ , or  $(0, K)$  if  $A < 0$ —is given by the position of the inflection point  $x_i(n)$  with respect to that range. In general, the shape in that range changes from decelerating to sigmoidal and then possibly

to accelerating as exponent  $n$  increases. However, reversals in that sequence may occur if  $\lambda h < 1$  (details not shown).

**Appendix B. Necessary and sufficient conditions for the existence of the interior predator–prey equilibrium  $E^*$**

We start with the particularly simple case of  $n = 0$ , such that predator’s functional response becomes independent of the prey density. Predators can establish if  $m < \lambda / (1 + \lambda h)$ , and they subsequently drive the entire system to collapse (i.e. both predators and prey die out deterministically). If the opposite inequality holds, predators go extinct and the prey population saturates in the boundary equilibrium  $E_s$  unless  $A > 0$  and the predators are introduced in such large numbers that they also drive the prey below the Allee threshold before both go extinct.

More generally, predators cannot establish if and only if

$$m > m_{max} = \frac{\lambda K^n}{1 + \lambda h K^n}. \tag{7}$$

On the other hand, the entire system certainly collapses if predators can establish and there is no interior equilibrium, i.e. if and only if  $A > 0$  and

$$m < m_{min} = \frac{\lambda A^n}{1 + \lambda h A^n}. \tag{8}$$

Inequalities (7) and (8) provide necessary and sufficient conditions for the interior predator–prey equilibrium to exist, i.e. we require  $m \in (m_{min}, m_{max})$  if  $A > 0$ . There is no such lower threshold in  $m$  if  $A \leq 0$  and therefore  $m_{min} = 0$ .

**Appendix C. Local stability of the interior equilibrium**

The derivation of inequalities (11)–(14) follows the same lines as outlined e.g. in Oaten and Murdoch (1975) and van Baalen et al. (2001). The determinant and trace of the Jacobian matrix  $J(x, y)$  associated with Eq. (1) equal

$$\text{Det } J(x, y) = myF'(x) - mg'(x) + F(x)g'(x),$$

$$\text{Tr } J(x, y) = -m + F(x) - yF'(x) + g'(x). \tag{9}$$

Substituting the values of  $E^* = (x^*, y^*)$  from (4) into (9) and simplifying, we get

$$\text{Det } J(x^*, y^*) = g(x^*)F'(x^*) > 0,$$

$$\text{Tr } J(x^*, y^*) = -\frac{g(x^*)}{m}F'(x^*) + g'(x^*). \tag{10}$$

The equilibrium  $E^*$  of (1) is thus locally asymptotically stable if and only if  $\text{Tr } J(x^*, y^*) < 0$ , i.e. if and only if

$$\frac{g'(x^*)}{g(x^*)} < \frac{F'(x^*)}{m}. \tag{11}$$

Using the functions  $g$  and  $F$  from Eq. (3) and the value of  $x^*$  from (5) we obtain that  $E^*$  is locally asymptotically stable, provided that it exists, if and only if:

$$\frac{x^*}{x^* - A} - \frac{x^*}{x^* + c} - \frac{x^*}{K - x^*} < n(1 - hm) - 1. \tag{12}$$

Thus,  $E^*$  remains stable and the paradox of enrichment cannot be obtained if and only if

$$\frac{x^*}{x^* - A} - \frac{x^*}{x^* + c} \leq n(1 - hm) - 1. \tag{13}$$

Finally, the paradox of enrichment cannot occur for any weak Allee effect if and only if

$$\frac{c}{x^* + c} \leq n(1 - hm) - 1. \tag{14}$$

Inequalities (13) and (14) follow from the fact that the expression on the left-hand side of (12) is an increasing function of both  $K$  and  $A$  that is maximized at  $K \rightarrow +\infty$  and  $A = 0$ , respectively (recall that weak Allee effects have  $A < 0$ ).

**Appendix D. Properties of the bifurcation curves**

For the branches of both predator invasion and simple extinction points,  $n$  is a decreasing function of  $m$  with an asymptote at  $m = 0$  if  $0 < A < 1$  or  $0 < K < 1$ , and an increasing function of  $m$  with an asymptote at  $m = 1/h$  if  $A > 1$  or  $K > 1$ . This gives five generic combinations of the two curves ( $0 < A < K < 1$ ,  $0 < A < 1 < K$ , and  $1 < A < K$  in Fig. 2A–C, and  $A \leq 0 < K < 1$ ,  $A \leq 0 < 1 < K$  in Fig. 2A–B with the dotted line absent).

It follows from (7) that the point  $A_r = K_r$ , in which four of the bifurcation branches are rooted in the  $(A, K)$  plane, increases with  $n$  if  $m < \lambda/(1 + \lambda h)$  and decreases otherwise. In the  $(m, A)$  plane,  $m_r$  increases with  $n$  if  $K > 1$  and decreases otherwise.

To show that for reasonably low  $n$  the Hopf bifurcation curve “moves to the left” in the  $(m, n)$  space as  $c$  decreases, we regard the curve as an implicit function of  $m$  and  $c$ :

$$f(m, c) = \frac{x^*}{x^* - A} - \frac{x^*}{x^* + c} - \frac{x^*}{K - x^*} - n(1 - hm) + 1 = 0. \tag{15}$$

Using the implicit function theorem and the chain differentiation rule, and taking into account Eq. (5) for  $x^*$ , we get

$$m'(c) = - \frac{\partial f / \partial c}{\partial f / \partial m} = \frac{-\frac{x^*}{(x^* + c)^2}}{nh + \frac{\partial}{\partial x^*} \left( \frac{x^*}{x^* - A} - \frac{x^*}{x^* + c} - \frac{x^*}{K - x^*} \right) \cdot \frac{\partial x^*}{\partial m}} = \frac{-\frac{x^*}{(x^* + c)^2}}{nh - \left( \frac{A}{(x^* - A)^2} + \frac{c}{(x^* + c)^2} + \frac{K}{(K - x^*)^2} \right) \frac{x^*}{mn(1 - hm)}}$$

The numerator is always negative as is the denominator provided  $n$  is not too large. Thus the root  $m(c)$  of the implicit equation (15) is an increasing function of  $c$  for sufficiently small  $n$ .

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