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RESEARCH ARTICLE

General Allee Effect in two-Species Population Biology

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Abstract

The main objective of this work is to present a general framework for the notion of the strong Allee effect in population models, including competition, mutualistic, and predator-prey models. The study is restricted to the strong Allee effect caused by an interspecific interaction. The main feature of the strong Allee effect is that the extinction equilibrium is an attractor. We show how a "phase space core" of three or four equilibria is sufficient to describe the essential dynamics of the interaction between two species that are prone to the Allee effect. We will introduce the notion of semistability in planar systems. Finally, we show how the presence of semistable equilibria increases the number of possible Allee effect cores.

Keywords: Population biology, competition models, Allee effect, semistability, extinction region.

1. Introduction

In their book, Courchamp et al. (2008) [4], the authors described the Allee effect in a straight forward manner: "The more the merrier: This effect is simply a causal positive relationship between the number of individuals in a population and their fitness. The more individuals there are (up to a point), the better they fare." So as population size approaches a threshold, favorable influences stimulate its growth and when it goes below it, unfavorable influences inhibit its growth. From their point of view, the Allee effect may be described as a notion of positive density dependence in which "the overall individual fitness, or one of its components, is positively related to population size or density" [4]. However, Lidicker (2010) [15] recently proposed that Allee effects be described and defined in terms of demographic processes. He explained that "Allee effects are expressed at the population level of organization, and the parameters of interest are the population properties of growth rates, recruitment rates, loss rates, equilibrium densities, and perhaps, success in establishing new populations". All the above authors indicated that they are using size and density interchangeably, unless otherwise explicitly stated.

Allee et al [1,2] provided experimental and field studies that confirmed the presence of the Allee effect among many species. The examples include bobwhite quails (*Colinus virginianus*) that huddle together to lower the surface presented to cold weather, and the disappearance of tsetse fly from an area in which the density of the flies fall below a threshold minimum density. (See also [11,13-16,19,20].)

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Let x_n denote the size or density of species x at time period or generation n . Then, we define the fitness of species x as the per-capita growth of its population, represented by the function $f(x_n) = x_{n+1}/x_n$. Thus, the difference equation that models the growth of the population is given by

$$x_{n+1} = x_n \cdot f(x_n) = g(x_n), \text{ with } g(x) \equiv x \cdot f(x), f \in C^3. \quad (1)$$

- *Definition:* Model (1) is said to have a *strong Allee effect* if the following conditions hold true:

- (i) $f'(x) > 0$ for $x \in (0, \varepsilon)$ for some $\varepsilon > 0$,
- (ii) $f(0) < 1$,
- (iii) There exists a unique $K > 0$, such that $f(K) = 1$, $f'(K) < 0$.

- *Remark:* It follows from the above conditions that there exists a fixed point A , $0 < A < K$, such that $f(A) = 1$ and A is unstable.

In the absence of the Allee effect, the fitness is expected to decrease when the population increases, most likely as the result of interspecific competition, difficulty in finding mates, or/and limitation of resources. On the other hand, a strong Allee effect is exhibited by an increase in per-capita growth with increasing population size. These competing mechanisms can be readily modeled for a single species x as follows. The fitness of the population is represented by the product

$$f(x) = f_0(x) \cdot I(x), \quad (2)$$

where $f_0'(x) < 0$, $I'(x) > 0$; $f_0(x)$ is the fitness function if there is no Allee effect, and $I(x)$ represents the Allee effect on the fitness of the population. The assumption $f_0'(x) < 0$ ensures the negative correlation of the fitness with the population size (in the absence of the Allee effect), i.e., the fitness decreases when the population increases (negative density dependence). On the other hand, $I'(x) > 0$ produces the required dynamics of Allee effect that may lead to extinction of the population if it falls below a certain threshold (positive density dependence).

An example of a model having the dynamics of (2) is the λ -Ricker Map [11],

$$x_{n+1} = x_n^\lambda \cdot \exp\{k - b x_n\}, \quad (3)$$

where $f_0(x) \equiv \exp\{k - b x\}$ and $I(x) \equiv x^{\lambda-1}$, $\lambda > 1$. The physical meaning of the exponent λ in (3) is given by the percentage rate of change $R_n \equiv \Delta x_n / x_n$ as follows

$$\lambda = \lim_{R_n \rightarrow 0} \frac{R_{n+1}}{R_n} = \lim_{R_n, x_n \rightarrow 0} \frac{d \log(x_{n+1})}{d \log(x_n)}. \quad (4)$$

This may be easily shown by taking the derivative of (3) near the fixed point $x=0$, i.e., $dx_{n+1}/dx_n = \lambda \cdot x_n^{\lambda-1} \exp(k)$ and then dividing this by (3), where we obtain $d \log(x_{n+1})/d \log(x_n) = \lambda$.

For two species models representing two species x and y , the difference equation is given by the planar system

$$\begin{aligned} x_{n+1} &= x_n \cdot f_1(x_n, y_n) = g_1(x_n, y_n) \\ y_{n+1} &= y_n \cdot f_2(x_n, y_n) = g_2(x_n, y_n). \end{aligned} \quad (5)$$

General planar models with the Allee effect caused by an interspecific interaction may be written in a form extending equation (2) to two-species model,

$$\begin{aligned}x_{n+1} &= x_n \cdot f_{0,1}(x_n, y_n) \cdot I_1(x_n) \\y_{n+1} &= y_n \cdot f_{0,2}(x_n, y_n) \cdot I_2(y_n) .\end{aligned}\tag{6}$$

Furthermore, extending the λ -Ricker model to two species, we get the following planar system

$$\begin{aligned}x_{n+1} &= x_n^{\lambda_1} \cdot \exp\{k_1 - b_1 x_n - c_1 y_n\} \\y_{n+1} &= y_n^{\lambda_2} \cdot \exp\{k_2 - b_2 x_n - c_2 y_n\} ,\end{aligned}\tag{7}$$

with $x_n > 0, y_n > 0$ and $\lambda_1, \lambda_2 > 0$.

For suitable selection of the parameters there can be up to seven fixed points:

- Origin: (0,0)
- Two fixed points on the x -axis, given implicitly by the roots of $e^{-k_1} = x^{\lambda_1-1} \cdot e^{-b_1 x}$, when $e^{-k_1} < (\lambda_1 - 1)/b_1$.
- Two fixed points on the y -axis, again given implicitly by $e^{-k_2} = y^{\lambda_2-1} \cdot e^{-c_2 y}$, when $e^{-k_2} < (\lambda_2 - 1)/c_2$.
- Two fixed points in the interior, given by the system $x^{\lambda_1-1} \cdot e^{-b_1 x} = e^{-k_1} e^{c_1 y}$ and $y^{\lambda_2-1} \cdot e^{-c_2 y} = e^{-k_2} e^{b_2 x}$. In the case of a symmetric model, i.e., $\lambda_1 = \lambda_2 \equiv \lambda$, $k_1 = k_2 \equiv k$, $b_1 = b_2 \equiv b$, $c_1 = c_2 \equiv c$, two fixed points exist in the interior, if $e^{-k} < (\lambda - 1)/(b + c)$.

Another interesting example of a planar model that describes a two species competition model exhibiting *contest inter-specific competition* [18] is the following [10].

$$\begin{aligned}x_{n+1} &= \frac{a_1 x_n^2}{1 + x_n^2 + b_1 y_n} \\y_{n+1} &= \frac{a_2 y_n^2}{1 + y_n^2 + b_2 x_n} ,\end{aligned}\tag{8}$$

with $x_n > 0, y_n > 0$, $a_{1,2}, b_{1,2} > 0$. This model may have up to nine fixed points:

- Origin: (0,0)
- Two fixed points on the x -axis, $x = \frac{a_1}{2} \pm \sqrt{\left(\frac{a_1}{2}\right)^2 - 1}$, when $a_1 > 2$.
- Two fixed points on the y -axis, $y = \frac{a_2}{2} \pm \sqrt{\left(\frac{a_2}{2}\right)^2 - 1}$, when $a_2 > 2$.
- Four fixed points in the interior. We can easily compute these fixed points for the symmetric case, where $a \equiv a_1 = a_2$ and $b \equiv b_1 = b_2$. They are given by $x = y = \frac{a-b}{2} \pm \sqrt{\left(\frac{a-b}{2}\right)^2 - 1}$, for $a > b + 2$, and $x = \frac{a+b}{2} \pm \sqrt{\left(\frac{a-b}{2}\right)^2 - 1 - b^2}$, $y = \frac{a+b}{2} \mp \sqrt{\left(\frac{a-b}{2}\right)^2 - 1 - b^2}$, for $a > b + 2\sqrt{1+b^2}$.

Next, we will introduce the notion of semistability in planar systems.

2. Semistability

Let us start by defining the notion of semistability in the one dimensional case.

- *Definition.* A fixed point x^* is said to be semistable if there exists an interval $I = (x^* - \delta, x^* + \delta)$, such that x^* is attracting from one side and repelling from the other side. It is said to be semistable from the left {right} if it is attracting on $(x^* - \delta, x^*)$ $\{ (x^*, x^* + \delta) \}$.

We will start our exposition by stating the main result of semistability for single species (one-dimensional maps).

- *Theorem 1* [6]. Consider the one-dimensional difference equation $x_{n+1} = g(x_n)$. If $g \in C^2$ and x^* is a fixed point of the map $g(x)$, such that $g'(x^*) = 1$ for $g''(x) \neq 0$, then x^* is semistable from the left if $g''(x) > 0$ and semistable from the right if $g''(x) < 0$. On the other hand, if $g'(x^*) = -1$, then the fixed point x^* is either asymptotically stable or unstable but not semistable.

Now we are going to study semistability for planar maps. Let us extend the notion of semistability to the two dimensional case by the following definition:

- *Definition.* A fixed point X^* is said to be semistable, if there exists a central manifold W^c that is semistable at X^* .

Let the map $G(x, y) = [g_1(x, y), g_2(x, y)]$, $G: R^2 \rightarrow R^2$. Let $JG(X^*)$ be the Jacobian matrix of G at the fixed point $X^* = (x^*, y^*)$. Then, the map G may be written in the form of the following difference equation

$$X_{n+1} = G(X_n) = JG(X^*) \cdot X_n + \tilde{G}(X_n), \quad (9)$$

where the map \tilde{G} contains all the higher order terms $\tilde{G}(X_n) \sim O(X_n^2)$ [12]. Let us assume that one of the eigenvalues of, say $\lambda_1 = 1$, and the other eigenvalues is $|\lambda_2| \neq 1$. Without loss of generality, we may assume that JG is the following diagonal matrix

$$JG = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}. \quad (10)$$

Now Eq. (9) may be written as

$$\begin{aligned} x_{n+1} &= \lambda_1 x_n + \tilde{G}_1(x_n, y_n) \\ y_{n+1} &= \lambda_2 y_n + \tilde{G}_2(x_n, y_n). \end{aligned} \quad (11)$$

The existence of a center manifold for Eq.(11) is guaranteed by the following theorem.

- *Theorem 2 (Invariant manifold theorem)* [3,16]. Assume that $|\lambda_1| = 1$ and $|\lambda_2| \neq 1$. For $|\lambda_1| = 1$ the eigenvector is E^c . Let us split the case of $|\lambda_2| \neq 1$ into two subcases, $|\lambda_2| > 1$ and $|\lambda_2| < 1$, where E^u and E^s are the corresponding eigenvectors. Suppose now that $F \in C^2$. Then there exist a center manifold W^c and a stable W^s (or an unstable W^u) manifold, respectively tangent to E^c and E^s (or E^u) at the fixed point $X=0$. Moreover, all the manifolds W^c , W^s and W^u are invariant (both positively and negatively invariant).

Now let the center manifold be given by $y = h(x)$. Throughout this section we consider the case where $\lambda_1 = 1$. Then substituting in Eq.(11), yields $x_{n+1} = u(x_n)$ where the map $u(x)$ is given by

$$u(x) \equiv x + \tilde{G}_1(x, h(x)), \text{ with } u'(x^*) = 1, \quad (12)$$

where x^* is the first component of the fixed point X^* . In order to have semistability on the center manifold $h(x)$ of the map $u(x)$, one must have, $u'(x^*) = 1$, and $u''(x^*) \neq 0$ (*Theorem 1*, [6]). We demonstrate the semistability by the two following examples for the two cases (i) $\lambda_2 < 1$, and (ii) $\lambda_2 > 1$. Furthermore, we provide two additional examples that show how this semistability may be destroyed if $u''(x^*) \neq 0$.

Example 1. Semistability with $\lambda_1 = 1$ and $\lambda_2 < 1$:

$$\begin{aligned} x_{n+1} &= x_n + y_n \\ y_{n+1} &= \frac{1}{2}y_n + \frac{1}{2}x_n^2 + y_n^2 + 2x_n y_n. \end{aligned} \quad (13)$$

We write the central manifold as $y = h(x)$, and substituting in (13) we obtain

$$\begin{aligned} x_{n+1} &= x_n + h(x_n) \\ y_{n+1} &= \frac{1}{2}h(x_n) + \frac{1}{2}x_n^2 + h(x_n)^2 + 2x_n h(x_n), \end{aligned} \quad (14)$$

that is

$$h(x + h(x)) = \frac{1}{2}h(x) + \frac{1}{2}x^2 + h(x)^2 + 2xh(x), \quad (15)$$

or

$$h(x + h(x)) = \frac{1}{2}h(x) - \frac{1}{2}x^2 + [x + h(x)]^2, \quad (16)$$

that is

$$h(H) - \frac{1}{2}h(x) = H^2 - \frac{1}{2}x^2, \quad (17)$$

where we set $H \equiv x + h(x)$. Then, we easily conclude that $h(x) = x^2$ by comparing both sides of (17). Now $H'(0) = 1$, $H''(0) = 2 > 0$, and thus, the central manifold is semistable from the left by *Theorem 1*.

Example 2. Semistability with $\lambda_1 = 1$ and $\lambda_2 > 1$:

$$\begin{aligned} x_{n+1} &= x_n + y_n \\ y_{n+1} &= 2y_n - x_n^2 + y_n^2 + 2x_n y_n. \end{aligned} \quad (18)$$

There is a unique fixed point $X^* = (0,0)$. Again, substituting $y = h(x)$ in (18) we obtain

$$\begin{aligned} x_{n+1} &= x_n + h(x_n) \\ y_{n+1} &= 2h(x_n) - x_n^2 + h(x_n)^2 + 2x_n h(x_n), \end{aligned} \quad (19)$$

that is

$$h(x + h(x)) = 2h(x) - x^2 + h(x)^2 + 2xh(x), \quad (20)$$

or

$$h(x + h(x)) = 2h(x) - 2x^2 + [x + h(x)]^2, \quad (21)$$

that is

$$h(H) - 2h(x) = H^2 - 2x^2, \quad (22)$$

where again we set $H \equiv x + h(x)$ and conclude that $h(x) = x^2$. Now $H'(0) = 1$, $H''(0) = 2 > 0$. Hence, the central manifold is semistable from the left by *Theorem 1*.

Example 3. $\lambda_1 = 1$ and $\lambda_2 < 1$ without semistability:

$$\begin{aligned} x_{n+1} &= x_n + x_n \cdot y_n \\ y_{n+1} &= \frac{1}{2} y_n + \frac{1}{2} x_n^2 + 2 y_n^2 + x_n^2 y_n^2, \end{aligned} \quad (23)$$

There is a unique fixed point $X^* = (0,0)$. We write the central manifold as $y = h(x)$, and substituting in (23) we obtain

$$\begin{aligned} x_{n+1} &= x_n + x_n \cdot h(x_n) \\ y_{n+1} &= \frac{1}{2} h(x_n) + \frac{1}{2} x_n^2 + 2 h(x_n)^2 + x_n^2 h(x_n)^2, \end{aligned} \quad (24)$$

that is

$$h(x + x \cdot h(x)) = \frac{1}{2} h(x) + \frac{1}{2} x^2 + 2 h(x)^2 + x^2 h(x)^2, \quad (25)$$

or

$$h(H) + h(x)(2x^2 - \frac{1}{2}) - 2h(x)^2 = H^2 + x^2(2x^2 - \frac{1}{2}) - 2(x^2)^2, \quad (26)$$

where we set $H \equiv x + x \cdot h(x)$. Again we conclude that $h(x) = x^2$. Equation (26) becomes $x_{n+1} = x_n + x_n^3 = g_1(x_n)$, where $g_1(0) = 0$, $g_1'(0) = 1$, $g_1''(0) = 0$, $g_1'''(0) = 6$. By a theorem in [9], if $g_1''(0) = 0$ and $g_1'''(0) \neq 0$, the fixed point $x = 0$ is unstable under the map $g_1(x)$. Hence, the center manifold W^c is unstable. Therefore, in order to obtain semistability, it is necessary to have $g_1''(0) \neq 0$.

Example 4. $\lambda_1 = 1$ and $\lambda_2 > 1$ without semistability:

$$\begin{aligned} x_{n+1} &= x_n + x_n \cdot y_n \\ y_{n+1} &= 2 y_n - x_n^2 + 2 y_n^2 + x_n^2 y_n^2. \end{aligned} \quad (27)$$

The reader may easily show that the central manifold W^c is $h(x) = x^2$, but similar to the previous example, we have $x_{n+1} = x_n + x_n^3 = g_1(x_n)$, with $g_1''(0) = 0$ and $g_1'''(0) \neq 0$, and thus, W^c is unstable again.

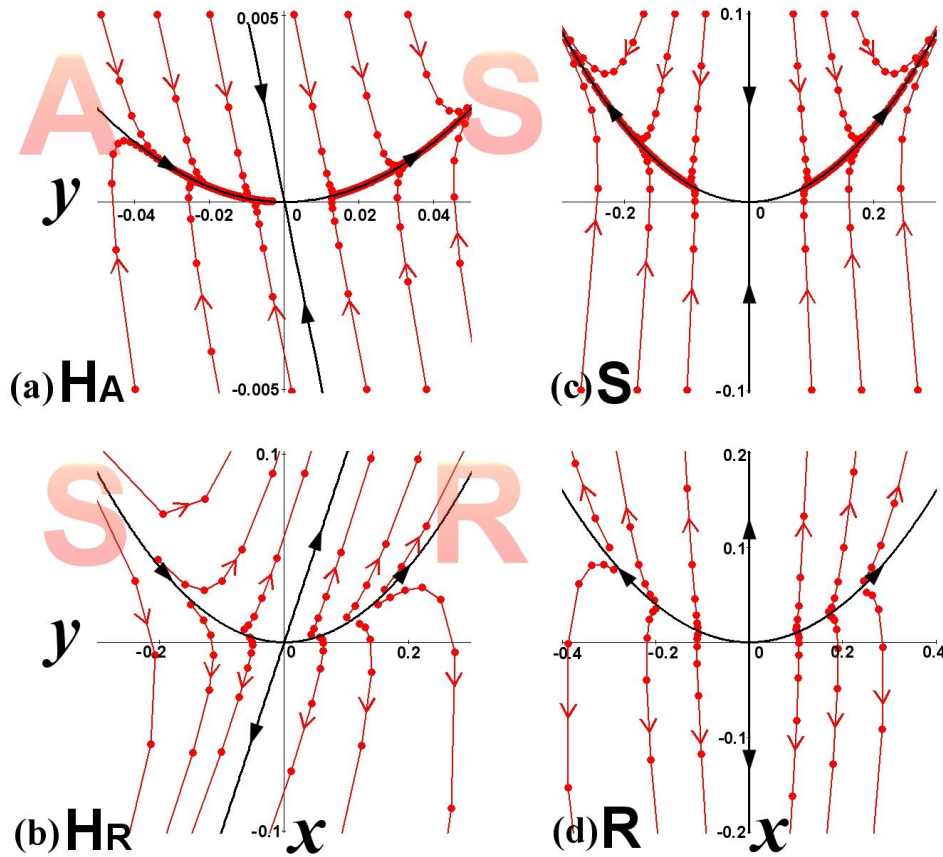


Figure 1. Phase space showing semistability (from the left) in accordance with the Examples 1-4. (a) Example 1: $\lambda_1 = 1$ (W^c), $\lambda_2 = 1/2 < 1$ (W^s). The left hand side of the phase space imitates an Attractor (A) and the right hand side a saddle point (S). The semistable point is indicated by H_A . (b) Example 2: $\lambda_1 = 1$ (W^c), $\lambda_2 = 2 > 1$ (W^u). The left hand side of the phase space imitates a saddle point (S) and the right hand side a Repeller (R). The semistable point is indicated by H_R . (c) Example 3 (without semistability): $\lambda_1 = 1$ (W^u), $\lambda_2 = 1/2 < 1$ (W^s). The fixed point is a saddle point (S). (d) Example 4 (without semistability): $\lambda_1 = 1$ (W^u), $\lambda_2 = 2 > 1$ (W^u). The fixed point is a Repeller (R).

- *Remarks:*

1. In the case of negative eigenvalues $\lambda_2 < 0$ we obtain the same dynamics but with oscillations. We omit the discussion of this case.
2. In the case of negative eigenvalue $\lambda_1 = -1$, the center manifold dynamics do not involve semistability as was explained earlier. The central manifold may be stable or unstable so that the fixed point in the plane is either a repeller (R), a saddle (S), or an attractor (A) (depending on the second eigenvalue).

In Figure 2 we demonstrate the creation of a semistable fixed point associated with $\lambda_1 = 1$ and (a) $\lambda_2 > 1$, (b) $\lambda_2 < 1$, by "merging" through bifurcation the two fixed points of stability R (or A) and S. The yellow shaded region in each panel shows the degenerated orbits of the discrete flow. In Figure 2(a) the degenerated orbits start near R, passing asymptotically near S, and diverge to infinity. As the R and S fixed

points are getting closer to each other (by setting suitably the map's parameters), the yellow regions shrink while the outer dynamics remain basically the same. The first eigenvalue that in our example operating on the horizontal axis, $\lambda_1 > 1$ on the left-hand side graph of the **R** fixed point, and $\lambda_1 < 1$ on the right-hand side graph of the **S** fixed point, approaches $\lambda_1 = 1$, where the bifurcation occurs. Similar explanation may be given for Figure 2(b). The degenerated orbits of the discrete flow come from infinity, passing asymptotically near **S**, and converge to **A**. The first eigenvalue $\lambda_1 < 1$, on the left-hand side graph of the fixed point **A**, and $\lambda_1 > 1$, on the right-hand side graph of the fixed point **S**, approaches $\lambda_1 = 1$ where bifurcation occurs. The second eigenvalue, operating on the vertical axis, retains its dynamics in this bifurcation, that is (a) $\lambda_2 > 1$ and (b) $\lambda_2 < 1$. Thus, the "created" semistable fixed points have $\lambda_1 = 1$ and (a) $\lambda_2 > 1$ or (b) $\lambda_2 < 1$, denoted by H_R or H_A , respectively.

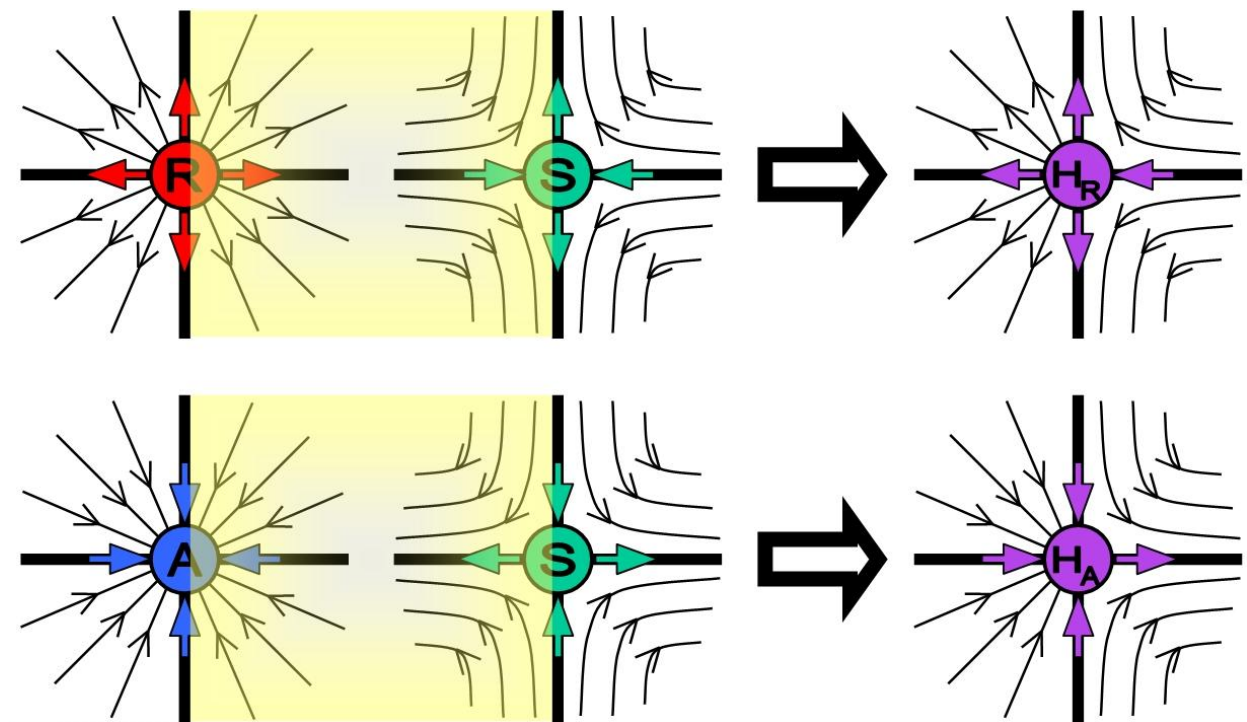


Figure 2. Two different types of semistable points H_R and H_A can be seen as "merging" two ordinary fixed points through a bifurcation, that is a repeller (**R**) + a saddle (**S**) (upper graphs) (see also Figure 1(b)), and an attractor (**A**) + a saddle (**S**) (lower graphs) (see also Figure 1(a)).

In all the above, we defined and described in detail, planar semistable fixed points that have only one eigenvalue that equals one ($\lambda_1 = 1$). Now we explore the cases when both eigenvalues equal one ($\lambda_1 = 1, \lambda_2 = 1$). Though this case will not be studied here, we will, however, demonstrate all the possible scenarios of this semistability. One possible combination is the utilization of **R** and **A** fixed points, as shown in Figure 3(a). The resulting semistable fixed point has both eigenvalues equal to one. The vertical axis is a separatrix, dividing the outward discrete flow on the left-hand side with the inward discrete flow on the right-hand side. For this reason, we denote this semistable fixed point as H_{RA} .

The three semistable fixed points H_R , H_A , and H_{RA} are created through a new type of bifurcation of the fixed points of regular stability R , A , and S (first generation semistability). More complicated structures may be obtained through the bifurcation of any two semistable fixed points (second generation semistability). As an example, we depict the case of the bifurcation of H_R and H_A in Figure 3(b). The result is a fixed point with different dynamical behavior in each quadrant. In particular, in the first quadrant the created fixed point behaves as an attractor A , while in the third quadrant as a repeller R ; in the second and fourth quadrants the fixed point behave as a saddle S . The dynamics of this semistable point is similar to H_{RA} . The main difference is that when H_{RA} is created through bifurcation of R and A (first generation semistability), the saddle behavior degenerates into a separatrix (coinciding with the vertical axis).

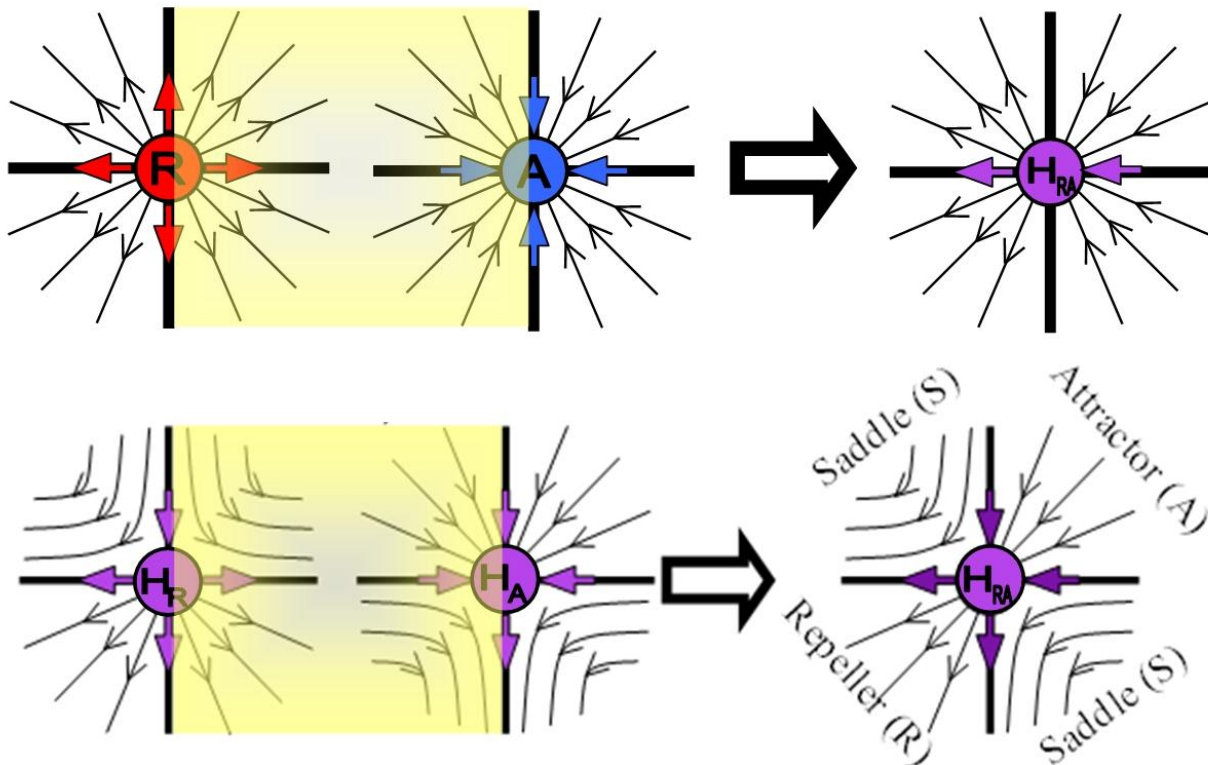


Figure 3. Semistable point H_{RA} is created through a bifurcation of the ordinary fixed points of stability R and A , or of the first-generation semistability points H_R and H_A . The semistable point H_{RA} on the top-right figure, is a special case of the semistable point H_{RA} depicted on the lower-right figure, where the second and fourth quadrants that behave as a saddle S degenerate to a separatrix (coinciding with the vertical axis) that consists entirely of fixed points.

- Remark:

In the case of eigenvalues $\lambda_1 = 1$ and $\lambda_2 = -1$, and if both of the central manifolds exist, then we will have the same dynamics as in the case of $\lambda_1 = 1$ and $\lambda_2 < 1$ (or $\lambda_2 > 1$), but with oscillations, leading again to the semistable fixed points H_A and H_R . This is due to the fact that the center manifold corresponding to $\lambda_2 = -1$ is either stable or unstable and cannot be semistable (*Theorem 1*).

In the sequel, we will utilize the fixed points R , A , S and H_R , H_A , H_{RA} to characterize the Allee effect in planar models.

3. General Allee effect

We start our approach by using the planar λ -Ricker map (5). In Figure 4 we plot the phase space for values of the parameters $\lambda_1 = \lambda_2 = 2$, $b_1 = b_2 = c_1 = c_2 = 1$, $k_1 = k_2 = 1.7$. There are seven fixed points, with an attractor A at the origin $(0,0)$, a pair of S and A at each axes, and a pair of R and S in the first quadrant. Furthermore, each species possess the strong Allee effect that is represented by the well-known one-dimensional Allee effect, located between the S fixed point on each axis and the attractor A at the origin. Moreover, we have two new fixed points, a repeller R , called *the planar Allee point*, and a saddle S , called *the planar carrying capacity*. The separatrices are heteroclinic orbits.

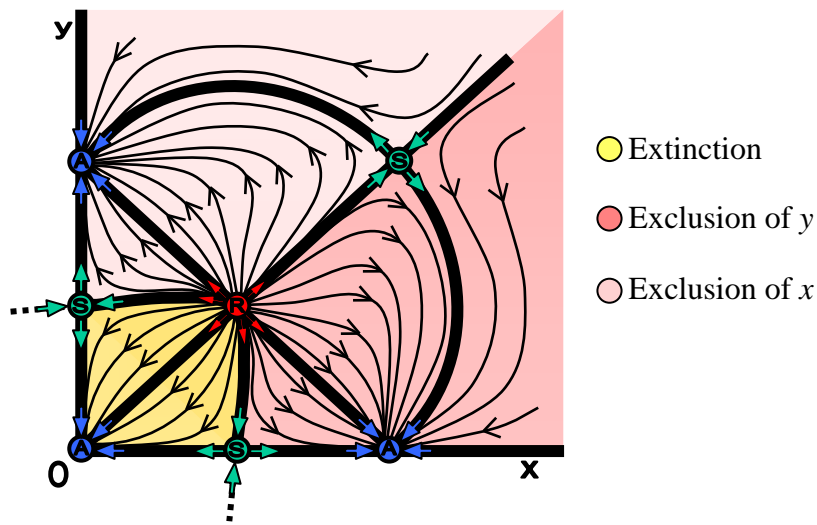


Figure 4. The phase space for the planar λ -Ricker map (5) with parameters $\lambda_1 = \lambda_2 = 2$, $b_1 = b_2 = c_1 = c_2 = 1$, $k_1 = k_2 = 1.7$ (symmetric map).

An interesting scenario occurs when two heteroclinic orbits connect two saddle points S on the two axes with an interior repeller point R (Figure 4). The two orbits lie on the stable manifolds of the saddle points on the axes. These two manifolds separate the extinction region (yellow) from the exclusion regions of species x (light red), and y (red). Notice that the boundary of the extinction region consists of the above mentioned two stable manifolds and the two axes x and y . Therefore, if the initial point (x_0, y_0) lies in the extinction region, then both species will go extinct. Now we formalize the above discussion.

- *Definition:* The planar *extinction region* or *Allee basin* is the basin of attraction of the origin; its boundary in the interior of the first quadrant defines the planar *Allee curve*. Moreover, a planar Allee point is any positive fixed point that lies on the planar Allee curve.

- *Remarks:*

1. Notice that the Allee curve encloses the extinction region, but not the two axes that correspond to one dimensional Allee effect and include only the Allee point.

2. An Allee point must be either of type R, S, or H, but cannot be of type A; this is self-evident, since then part of the extinction region will be in the basin of attraction of the Allee point A, an absurdity.
3. The notions of planar Allee curve and planar Allee point generalize, in a natural way, the Allee point threshold point in the (1-dimensional) dynamics of single species.
4. The planar extinction region generalizes the one-dimensional extinction interval of each species that is each axis segment bounded by the origin and the 1-dimensional Allee point S.
5. The certain arrangement of the four fixed points located on the boundaries of the extinction region (e.g., A-S-R-S in Figure 4) is not random. On the contrary, this certain permutation of fixed points is valuable for having the Allee effect and it is called “core” of the Allee effect. In the next section we will expose all the possible arrangements of fixed points that construct a core.

The planar Allee point R in the above remarks leads to the following definition.

- *Definition:* A planar competition model is said to possess the strong Allee effect properly if its phase space exhibits an extinction region and a non-extinction region separated by an Allee curve.

We now resume our investigation of the planar map (8) of two competing species exhibiting *contest inter-specific competition*. As we mentioned, depending on the parameter values we may have nine fixed points (see Introduction). A diagram of the phase space is given in Figure 5 for $a_1 = 2.5$, $a_2 = 2.5$, $b_1 = 0.1$, $b_2 = 0.1$. We observe the presence of an Allee curve that passes through three planar Allee points (similar to Figure 4). Two of the planar Allee points are the fixed points S that correspond to 1-dimensional Allee points (placed on the axes); the third Allee point is the interior fixed point R. In addition, the two 1-dimensional carrying capacities points A are present. The interior saddle point S in Figure 4, that is changed to A in Figure 5, is a planar carrying capacity point. Moreover, in Figure 5 there are two new interior S fixed points surrounding the mentioned planar carrying capacity point A. Both the interior saddle points S and the attractor A are characterized by a stable manifold emanating from the R Allee point. Therefore, we give the following definition for the planar carrying capacity curve and points.

Definition: A planar carrying capacity is a fixed point with one stable manifold emanating from an Allee point. The planar *carrying capacity curve* may connect all or a subset of the planar carrying capacities. The dynamics of the planar carrying capacities have to be A, S, or H, and not R (since R has no stable manifolds).

The two planar carrying capacities S (Figure 5) separate the exclusion regions from the coexistence region. It is noteworthy to mention that the four regions of (1) extinction (yellow), (2) exclusion of species y (red), (3) exclusion of species x (light red), and (4) coexistence (light blue), are either the basin of attraction of A fixed points or the stable sets of H fixed points.

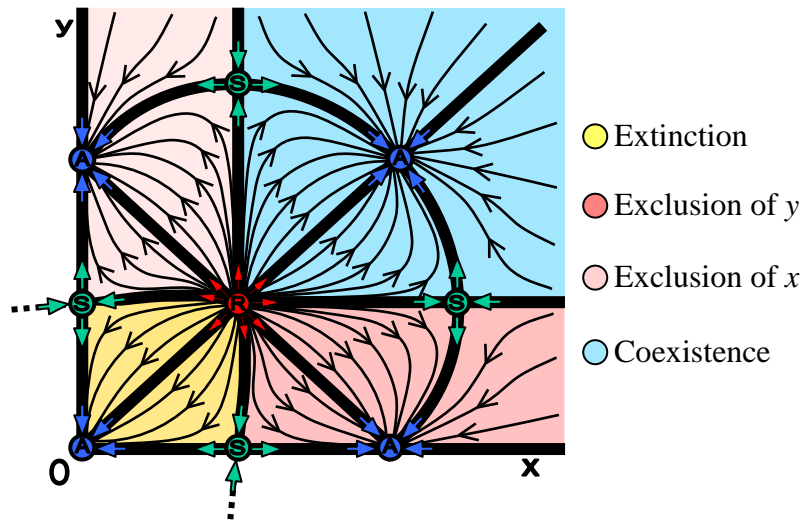


Figure 5. The phase space for the planar map of (8) (competition model that exhibits *contest inter-specific competition*) and a selection of the parameter values $a_1 = a_2 = 2.5$, $b_1 = b_2 = 0.1$ (symmetric map).

Generally speaking, planar maps may exhibit only two of the critical regions of extinction, exclusion, and co-existence. The example in Figure 4 shows a case with extinction and exclusion regions, while for planar maps that do not exhibit strong Allee effect there are only exclusion and coexistence regions. Theoretically, we may be able to observe phase spaces with only extinction and coexistence regions, as shown in Figure 6. This is the phase space of Figure 4, after exchanging the S carrying capacity points to A , and vice versa.

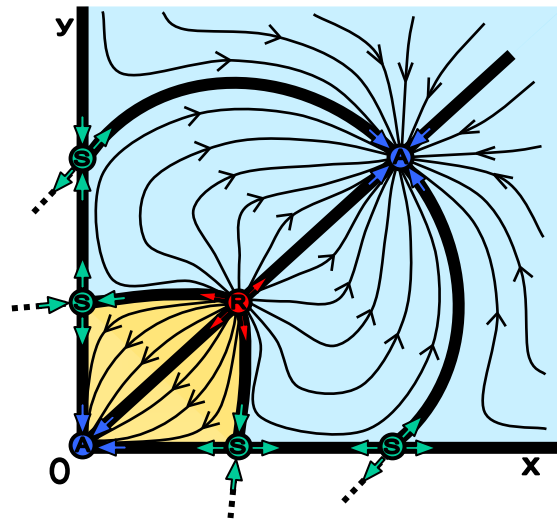


Figure 6. A hypothetical phase space with only extinction and coexistence regions.

Moreover, Figure 7 demonstrates how the Allee point R merges with the carrying capacity S through a bifurcation, by varying suitably the parameters (while keeping the symmetry of the system). The result of the bifurcation is a semistable fixed point H_R , as defined in Section 2. The core is still present but is constructed by different permutation of fixed points since R is replaced by H_R .

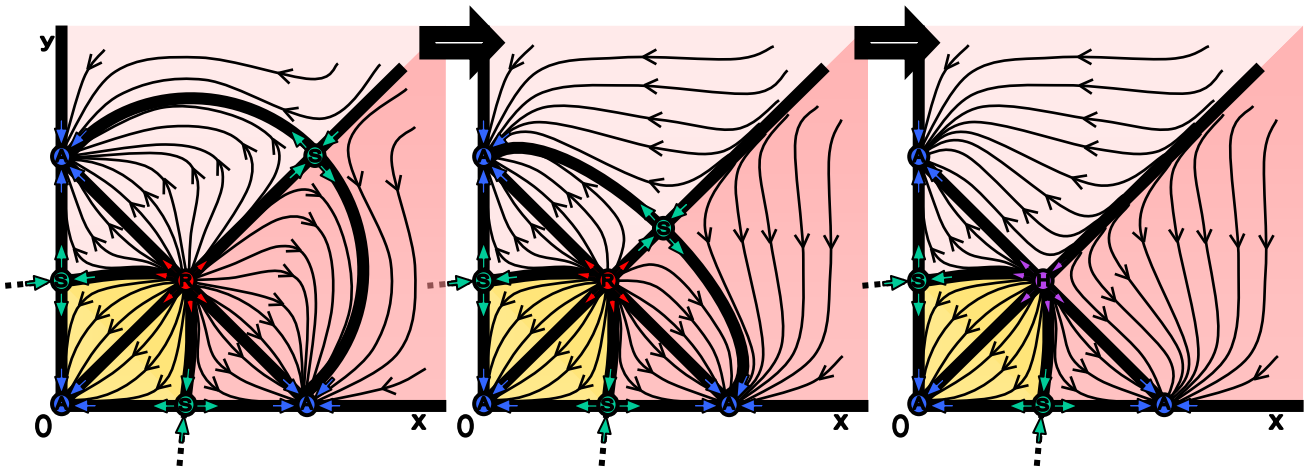


Figure 7. In the symmetric planar λ -Ricker map, the two interior fixed points of a repeller (R) and a saddle (S) are merged through a bifurcation into one semistable fixed point when $k=\ln(2)$. Panels show a gradual decrease of k :(a) $k=1.7$, (b) $k=1$, (c) $k=\ln(2)$. The generated semistable point (indicated by H) is of type H_R (see Figure 2).

Notice that in the case of the symmetric planar λ -Ricker map, the semistable point in the interior appears for $k = \ln[(b+c)/(\lambda-1)]$. For other selections of the parameters, the two fixed points on each of the axes may be merged through a bifurcation into a semistable point. The bifurcation leads to a semistable fixed point H_A . For the symmetric λ -Ricker map, this occurs when $k = \ln[b/(\lambda-1)]$ for the x -axis and $k = \ln[c/(\lambda-1)]$ for the y -axis. Figure 8 shows a hypothetical case where all three semistable points (two H_A fixed points at each axis and one H_R fixed point in the interior) appear simultaneously.

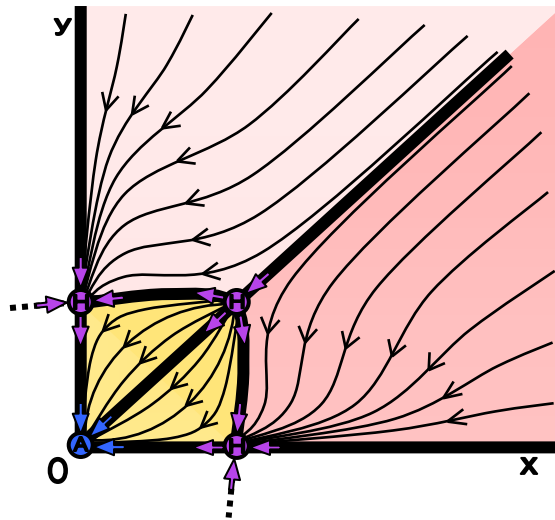


Figure 8. Phase space with three semistable points (indicated by H), two H_A fixed points at each axis and one H_R fixed point in the interior.

Finally, we are in a position to give details and explanations of the notion of the "core" of the Allee effect.

4. The core of Allee effect

Different arrangements of the surrounding fixed points may lead to different cores of the Allee effect. Figure 9 shows the three possible different cores of the Allee effect, one with three fixed points (A-R-S) and two with three fixed points (A-S-R-S, A-R-S-R).

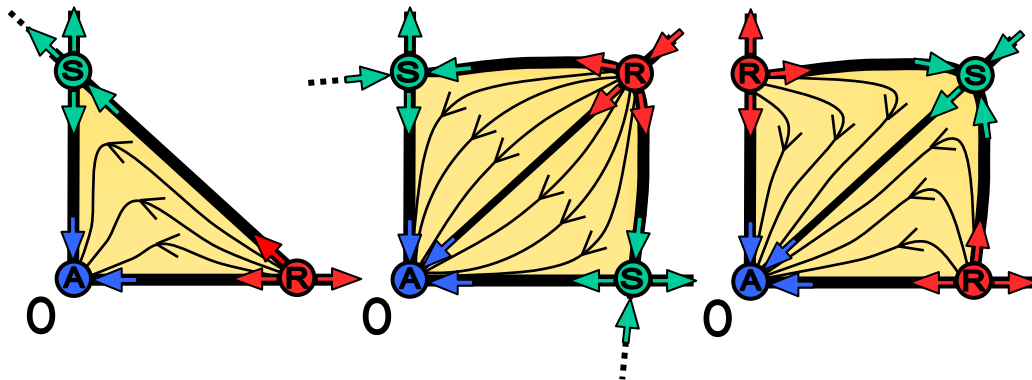


Figure 9. The three possible arrangements of fixed points that construct a core of the Allee effect.

The semistable fixed points H_R , H_A , and H_{RA} increase the possible permutations of the core. This can be realized in two possible ways. (i) By replacing fixed points of regular stability A, R, S; (ii) Having double role as fixed points. For example, in the upper panels of Figure 10 we observe semistable fixed points H_R and H_A replacing regular fixed points R and S, respectively. However, in the lower panels we observe the double role of H_R (as R and S) and H_A (as A and S).

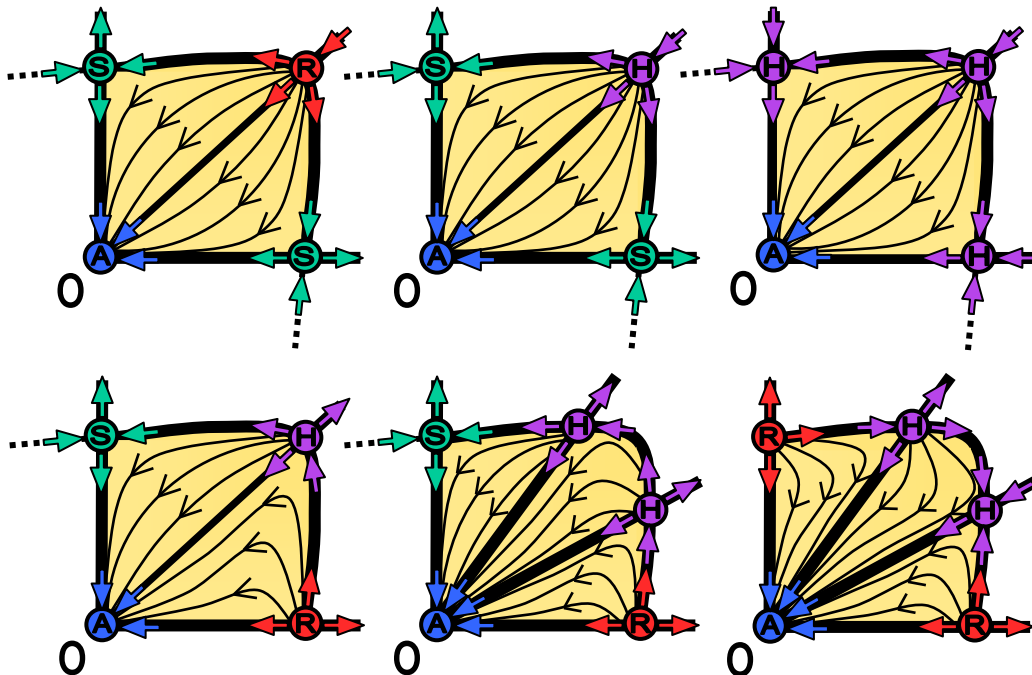


Figure 10. Semistable fixed points H_R and H_A replace regular fixed points R and S, respectively, as it is shown in upper middle and right panels. The double role of H_R (as R and S) and H_A (as A and S) is shown in the lower panels. (Both H_R and H_A are indicated by H.)

5. Discussion and conclusions

In [4] the authors laid down the consequences of Allee effects for population and community dynamics. We see at least two fruitful avenues for future research on Allee effect. The first avenue is to learn much more about effects of positive density dependence on population dynamics by recognizing and modeling impacts of multiple Allee effects, i.e., in two or more fitness components [4]. The second avenue, which is more relevant to this paper, is to investigate the Allee effect for multi-species systems.

In a series of papers, Deredec and Courchamp [7,8] studied the impact of Allee effect on host populations in a host-parasitoid systems. Like most of the literature on population dynamics (e.g., [5]), they used differential equations for modeling populations with Allee effect.

In this paper, we have developed a theoretical foundation for discrete models of populations with strong Allee effect, described by difference equations. These models describe populations that exhibit a "critical size" below which the population declines on average and goes to extinction, and above which it increases on average. To illustrate our concepts, we investigated two planar models with Allee effect and showed all the related possible scenarios of phase space diagrams. These are (i) the λ -Richer competition model, and (ii) a specific model of contest inter-specific competition. These models belong to a class of systems that possess "intraspecific" Allee effect, in which the Allee effect is caused by the intraspecific competition (competition among members of the same species), and not by the interspecific competition (competition between individuals of different species). This work may be applicable to both intraspecific and interspecific competition models.

Moreover, we presented a general framework for the notion of strong Allee effect in planar discrete semi-dynamical systems but restricted to the dynamics of equilibria, as shown by the following four paragraphs:

- A significant idea in the paper is the introduction of the "Allee curve", which is the boundary of the basin of attraction of the origin (0,0) that separates the extinction region from the rest of the phase space, and thus generalizing the concept of "Allee-point" in one-dimensional dynamics.

- We described the essential dynamics that characterize the strong Allee effect within the basin of attraction of the origin that is bounded by the Allee curve. This is called the "phase space core" of the Allee effect and consists of only 3 or 4 fixed points. The regular type of fixed points (repeller, saddle, attractor) combine three different types of cores. However, semistable fixed points increase the variety of "phase space cores".

- We introduced and thoroughly characterized the notion of semistability in planar discrete semi-dynamical systems, and showed its crucial role in the Allee effect dynamics. Two categories of semistable fixed points are defined, and their phase spaces are studied in accordance with the regular type of fixed points.

In a future work, we will investigate thoroughly the dynamics of both scrambled competition models with strong Allee effect and contest competition models with strong Allee effect. Moreover, we will study the cases of periodic orbits in the presence of strong Allee effect.

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