Bifurcation as the Source of Polymorphism

Ernest Barany

New Mexico State University, Las Cruces, NM 88001, USA
`ebarany@nmsu.edu`

Abstract. In this paper we present a symmetry breaking bifurcation-based analysis of a Lotka-Volterra model of competing populations. We describe conditions under which equilibria of the population model can be uninvadable by other phenotypes, which is a necessary condition for the solution to be evolutionarily relevant. We focus on the first branching process that occurs when a monomorphic population loses uninvadability and ask whether a symmetric dimorphic population can take its place, as standard symmetry-breaking scenarios suggest. We use Gaussian competition functions and consider two cases of carrying capacity functions: Gaussian and quadratic. It is shown that uninvadable dimorphic coalitions do branch from monomorphic solutions when carrying capacity is quadratic, but not when it is Gaussian.

Keywords: Symmetry breaking bifurcation, population model, evolutionary stability.

1 Introduction

Polymorphic population models, that is models in which organisms with more than one value of a specified physical trait can coexist asymptotically in time, can arise from models that allow only organisms with a single specified trait value via steady state bifurcations. The states in these bifurcations are the physical traits and the bifurcation parameters are environmental variables. This kind of phenomena is typical of systems that exhibit *spontaneous symmetry breaking.* Since it is known that spontaneous symmetry breaking is generic for systems with symmetry [1] (as many common population models such as the Levene model or the Lotka-Volterra models do), the possibility presents itself that speciation processes may be driven by symmetry breaking bifurcations. The process by which a population can split is referred to as *disruptive selection* by biologists (see the review by [2]) who often study the evolutionary mechanisms of branching using complicated stochastic "individual-based" simulations. The work in this paper shows that many features of population equilibrium models are fixed by the stability properties of the deterministic dynamical model.

In this paper we present a bifurcation-theoretic analysis of a Lotka-Volterra model to show how the possibility of stable branching from a monomorphic population to dimorphic depends on the details of the competition and carrying capacity functions. In particular, we consider Gaussian competition functions as

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is commonly done, and take two cases for carrying capacity functions: Gaussian and a quadratic function. An interesting feature is that though the two carrying capacity models are essentially identical at quadratic order, so that the local bifurcation behavior near the origin of phenotype space might be expected to be similar. In fact, the two cases give quite different results.

The basic model under consideration can be written

$$\frac{dn_j}{dt} = r_j[K(x_j) - \sum_{k=1}^{M} C(x_j, x_k)n_k]n_j, \qquad (1)$$

where $j = 1, 2, \ldots, M$ indexes the competing phenotypes, and n_j is the population of organisms that have phenotype x_j, which we assume to be a real number. The functions $C(x_j, x_k)$ describe competition between the j^{th} and k^{th} phenotypes and the function $K(x_j)$ gives the carrying capacity for the j^{th} phenotype; these functions will be discussed below. The function r_j is the growth rate, which has been scaled by $K(x_j)$ relative to a normal logistic model in order to simplify the analysis. Since the basic growth rates and the carrying capacity are all positive, it follows that the r_j's have no effect on the stability issues which are the main topic of this analysis.

We are interested in describing the simplest splitting event: monomorphism to dimorphism. Therefore it is sufficient to consider a model with three competing phenotypes (*i.e.*, $M = 3$), though the results presented for this case generalize to arbitrary M. More competitors can lead to different long term results, and can alter the rate at which the morphic types of the population change, but if the phenomenon of an uninvadable dimporhism cannot occur for three competitors, it will not be able to occur no matter how many competitors exist, so the present analysis can be thought of as a necessary conditition for branching that any more realistic model must be consistent with.

The remainder of this section will be organized as follows. First, general expressions will be derived for the eigenvalues of the jacobian of the system for monomorphic and dimorphic populations in terms of the as yet unspecified competition and carrying capacity functions. Then the idea of invadability of asymptotically stable equilibria will be discussed. Finally, detailed analyses will be presented for specific competition and carrrying capacity functions to show that the possibility of stable branching depends on the specifics of these functions.

2 Stability and Invadability of Equilibria

Before proceeding, we note a property of (1), namely *symmetry* [1]. This term refers to a specific mathematical property that has profound effects, but which will be used only cursorily here. The basic operation of symmetry in this context amounts to the relabeling of phenotypes, which can be thought of as a permutation of the M indices. Mathematically, the set of such rearrangements comprises the group S_M of permutations on M objects. The key observation is that the set of M equations (1) is invariant under the operations of S_n. That is, the particular equations are permuted among themselves in the same way that the indices are permuted.

The usefulness of this observation in the current case is that it means that all equilibrium solutions with a fixed number of nonzero phenotypes, (for example, all monomorphic solutions) are equivalent, in that each such solution is the image of all other such solutions under the action of some element of S_n (just pair-wise interchanges in the monomorphic situation). Therefore, only one such solution need be analyzed, say the solution with $n_1 = K(x_1)$ and all other $n_j = 0$. Similarly only one dimorphic solution need be studied, say the one with n_1 and n_2 nonzero.

2.1 Monomorphism

The local stability of the monomorphic solution $n_j^{Mon} = K(x_j)\delta_{j1}$ is determined by the eigenvalues of the jacobian matrix evaluated at the monomorphic equilibrium:

$$J^{Mon} = \begin{pmatrix} -2r_1K(x_1) & -r_1C(x_1,x_2)K(x_1) & -r_1C(x_1,x_3)K(x_1) \\ 0 & r_2(K(x_2) - C(x_2,x_1)K(x_1)) & 0 \\ 0 & 0 & r_3(K(x_3) - C(x_3,x_1)K(x_1)) \end{pmatrix} \tag{2}$$

which are just the diagonal elements of the matrix, since it is triangular.

The $(1,1)$ element of J^{Mon} is clearly negative, and amounts to the fact that if an organism with any phenotype is introduced into the environment with no other organisms present, the population will grow. The $(2,2)$ and $(3,3)$ elements contain the same information as each other, which refers to whether an invading phenotype x_2 or x_3 can out-compete a resident population with phenotype x_1. That is, the condition that a resident with phenotype x will be stable against invasion by a phenotype y can be written

$$\Lambda^{Mon}(x,y) = K(y) - C(y,x)K(x) < 0. \tag{3}$$

Note that this result is the same as would be obtained for any number of competitors M.

A property of particular interest is whether the monomorphic equilibrium is *uninvadable*, see, *e.g.,* [3], which will be so for some phenotype $x = x^*$ if the condition (3) holds for all $y \neq x^*$. Note that $\Lambda^{Mon}(x,x) = 0$ for all x, which is intuitively obvious since it amounts to the statement that “invasion” by an identical phenotype can always occur, so a necessary condition for phenotype x^* to be uninvadable is that the function $\Lambda^{Mon}(x^*,y)$ have a critical point as a function of y for $y = x^*$, that is,

$$\frac{\partial \Lambda}{\partial y}(x^*,y)|_{y=x^*} = 0. \tag{4}$$

Moreover, the critical point x^* will, in fact, be univadable if the local extremum is a maximum, that is, if

$$\frac{\partial^2 \Lambda}{\partial y^2}(x^*, y)|_{y=x^*} < 0, \tag{5}$$

and will be invadable by all nearby phenotypes if the opposite sign condition holds. Examples for specific cases will be shown below, but a useful property that holds for a wide class of competition functions can be seen as follows. We assume that $C(y,x) \leq 1$ for all phenotypes x, y and that equality hold only for $y = x$. This is not a strong assumption and can be thought of a a normalization condition since species with the same phenotype will be maximally competitive. Under this assumption, $\frac{\partial C}{\partial y}(y,x)|_{y=x} = 0$, and a necessary condition for any such competition function (such as a Gaussian function) to allow the existence of an uninvadable monomorphism x^*, is that x^* must be a critical point of the carrying capacity function,

$$K'(x^*) = 0. \tag{6}$$

and a sufficient condition for uninvadability is that

$$\frac{\partial^2 \Lambda^{Mon}}{\partial y^2}(x^*, y)|_{y=x^*} = K''(x^*) - \frac{\partial^2 C}{\partial y^2}(y, x^*)|_{y=x^*} K(x^*) < 0. \tag{7}$$

The opposite sign condition indicates that a resident population with phenotype x^* can be invaded by all nearby phenotypes.

2.2 Dimorphism

We next present an analysis that parallels the previous case for the case of dimorphic solutions. As above, we assume that only phenotypes x_1 and x_2 have nonzero populations, the analysis for other pairs of nonzero populations is equivalent. The solution can easily be found to be

$$n_1^{Di} = \frac{K(x_1) - C(x_1,x_2)K(x_2)}{1 - C(x_1,x_2)C(x_2,x_1)} \tag{8}$$

$$n_2^{Di} = \frac{K(x_2) - C(x_2,x_1)K(x_1)}{1 - C(x_1,x_2)C(x_2,x_1)} \tag{9}$$

$$n_3^{Di} = 0. \tag{10}$$

Note that the numerators of the nonzero populations are identical to the stability eigenvalue function Λ^{Mon}, above, so that the dimorphic solution becomes feasible (positive) when the monomorphic solution loses stability. This is the signal of a transcritical bifurcation.

After some simplification, the jacobian matrix at the dimorphic solution can be written

$$J^{Di} = \begin{pmatrix} -r_1 n_1^{Di} & -r_1 C(x_1,x_2) n_1^{Di} & -r_1 C(x_1,x_3) n_3^{Di} \\ -r_2 C(x_2,x_1) n_2^{Di} & -r_2 n_2^{Di} & -r_2 C(x_2,x_3) n_2^{Di} \\ 0 & 0 & r_3(K(x_3) - C(x_3,x_1)n_1^{Di} - C(x_3,x_2)n_2^{Di}) \end{pmatrix} \tag{11}$$

Two of the stability eigenvalues of the dimorphic equilibrium are the eigenvalues of the 2×2 matrix

$$\begin{pmatrix} -r_1 n_1^{Di} & -r_1 C(x_1, x_2) n_1^{Di} \\ -r_2 C(x_2, x_1) n_2^{Di} & -r_2 n_2^{Di} \end{pmatrix} \tag{12}$$

which are easily seen to be positive as long as n_1^{Di} and n_2^{Di} are positive and $C(x_1, x_2) < 1$ as long as $x_1 \neq x_2$. The third eigenvalue measures the ability of a third phenotype (say z) to invade an existing dimorphic population (with phenotypes x and y), and its sign is determined by the function

$$\Lambda^{Di}(x, y, z) = K(z) - \frac{C(z,x) - C(z,y)C(y,x)}{1 - C(x,y)C(y,x)} K(x) - \frac{C(z,y) - C(z,x)C(x,y)}{1 - C(x,y)C(y,x)} K(y). \tag{13}$$

As before, note that for fixed x and y, $\Lambda^{Di}(x, y, x) = \Lambda^{Di}(x, y, y) = 0$, so again, in order for a dimorphic population with phenotypes x^* and y^* to be uninvadable by a third phenotype z, it must be true that $\Lambda(x^*, y^*, z)$ viewed as a function of z must have critical points for $z = x^*$ and $z = y^*$, and they must be local maxima. Before considering specific examples, we consider some issues of a general character relative to the issue of critical behavior for dimorphic solutions which is a necessary condition for uninvadability. We assume that the competition functions $C(x, y)$ obey the conditions $C(x, y) = C(y, x)$ and $\frac{\partial C}{\partial x}(x, y) = -\frac{\partial C}{\partial y}(x, y)$, which are true for many important special cases, such as any function that depends on x and y through the quantity $(x - y)^2$, *i.e.*, $C(x, y) = C((x - y)^2)$, of which a Gaussian function is a familiar special case. Under these assumptions, there is always a class of symmetric dimorphic solutions that satisfies $y^* = -x^*$, and for definiteness and simplicity, we will focus on these solutions in this paper. For the symmetric branching solution, he stability eigenvalue becomes

$$\Lambda^{Di*}(x, z) = K(z) - \frac{C(z,x) + C(z,-x)}{1 + C(x,-x)} K(x), \tag{14}$$

and in this case, the two criticality conditions become identical. Specifically, if $C^* = C(-x^*, x^*)$ and $C^{*'} = \frac{\partial C}{\partial y}(y, x^*)|_{y=-x^*}$, then the critical value x^* must satisfy

$$K'(x^*) - \frac{C^{*'}}{1 + C^*} K(x^*) = 0. \tag{15}$$

Further, if $C^{*''} = \frac{\partial^2 C}{\partial y^2}(y, x^*)|_{y=-x^*}$ and $C^{0''} = \frac{\partial^2 C}{\partial y^2}(x^*, x^*)$, a sufficient condition that ensures that the critical points defined by (2.2) describe an uninvadable dimorphism is

$$K''(x^*) - \frac{C^{0''} + C^{*''}}{1 + C^*} K(x^*) < 0, \tag{16}$$

and if the opposite sign condition holds then all nearby phenotypes can invade the dimorphism.

As a final comment in this section, we mention that including more competitors in the system (1) does not change the previous conclusions. Additional eigenvalues occurring in such cases are equivalent to Λ^{Di}.

3 Gaussian Competition Functions

In the previous section, we derived conditions for univadable monomorphism and uninvadable dimorphism in an ecological models of competing populations with particular values of some phenotype. So far, no assumptions whatsoever have been made about the carrying capacity function $K(x)$, and only minimal assumptions about the competition functions $C(x, y)$, specifically that C is a function of the square of the distance in phenotype space $C(x, y) = C((x - y)^2)$, and that $C(x, x) = 1$ for all phenotypes x. To proceed, we must be more specific. In this paper we will take the approach of specifying the competition function once and for all, and then considering various subcases of carrying capacity. In particular, we will assume the competition function to be Gaussian $C(x, y) = e^{\frac{-(x-y)^2}{2\sigma_C^2}}$, as is commonly done in the biological literature [4,5]. In this case, the conditions for existence of uninvadable mono- and dimorphism are given below. Recall from above that for each class of polymorphism, there are two conditions: a criticality condition in the form of an equation that a phenotype corresponding to an uninvadable population must satisfy which in practice is what must be solved for x^*, and an inequality that states that the curvature of the eigenvalue at the critical point is such that the critical phenotype is a local maximum of the eigenvalue.

3.1 Univadable Monomorphism

$$\text{Criticality: } K'(x^*) = 0 \tag{17}$$

Recall that this condition for uninvadability depends only on the requirement that $C(x, x) = 1$ for all x.

$$\text{Curvature: } K''(x^*) + \frac{1}{\sigma_C^2} K(x^*) < 0 \tag{18}$$

3.2 Uninvadable Dimorphism

$$\text{Criticality: } K'(x^*) - \frac{x^*}{\sigma_C^2} \left(\tanh(\frac{x^{*\,2}}{\sigma_C^2}) - 1 \right) K(x^*) = 0 \tag{19}$$

$$\text{Curvature: } K''(x^*) + \frac{2x^*}{\sigma_C^2} K'(x^*) + \frac{1}{\sigma_C^2} K(x^*) < 0 \tag{20}$$

4 Gaussian Carrying Capacity: Competitive Exclusion Principle

We now specialize to Gaussian carrying capacity functions. That is, we will consider the two carrying capacity functions

$$K_G^{(1)}(x) = K_0 e^{\frac{-x^2}{2\sigma_K^2}} \tag{21}$$

which describes a single Gaussian distribution centered about the location $x = 0$ (chosen without loss of generality). There is a great deal of work on the model above. This is a classic example where the competitive exclusion principle would be expected to hold, wherein two species competing for a single resource must result in one species outcompeting the other. We will see that monomorphic uninvadability can happen in this context, but this univadable state can also lose stability as ecological parameters are varied, and, as we will see, no uninvadable dimorphism exists emerges to take its place.

From (17), the only possible uninvadable phenotype is $x = 0$, and the curvature condition there is

$$\frac{1}{\sigma_C^2} - \frac{1}{\sigma_K^2}, < 0 \tag{22}$$

that is, the state that maximizes the carrying capacity is uninvadable as long as the variance of the carrying capacity is less than the variance of the competition function. This is well known in the biology literature, [6,4]. If we define the ecological parameter whose variation we study to be $\rho = (\frac{\sigma_K}{\sigma_C})^2$, the condition for an uninvadable monomorphism at $x = 0$ to exist can be written $\rho < 1$. This is a well known result.

Next we consider dimorphic solutions. Recall that dimorphic solutions become asymptotically stable in the subspace associated with the dimorphic phenotypes when the monomorphic solution loses asymptotic stability. As mentioned previously, this occurs by virtue of a transcritical bifurcation as ρ crosses one. However, as we will see, none of the symmetric dimorphisms can possibly be uninvadable, meaning that when the monomorphic solutions become unstable due to variation of a parameter, no stable, univadable dimorphism emerges from a branching event as we will see does occur in the two resource case.

To see all this, note that the condition (19) that determines possible critical symmetric dimorphisms x^* becomes

$$\frac{K'(x^*)}{K(x^*)} = -\frac{x^*}{\sigma_K^2} = \frac{1}{\sigma_C^2}[\tanh(\frac{x^{*\,2}}{\sigma_C^2}) - 1] \tag{23}$$

which can be solved to obtain

$$x^* = \frac{\sigma_C}{\sqrt{2}}\sqrt{\ln(\frac{2\sigma_K^2 - \sigma_C^2}{\sigma_C^2})} = \frac{\sigma_C}{\sqrt{2}}\sqrt{\ln(2\rho - 1)} \tag{24}$$

from which it is seen that the critical symmetric dimorphic solution exists only if $\rho > 1$, which is the same as the condition for the monomorphism with $x = 0$ to become unstable. The curvature condition for uninvadability of the symmetric dimorphism at x^* can be written

$$\frac{K(x^*)}{\sigma_K^2}[\rho - 1 + \ln(2\rho - 1)\frac{1-2\rho}{2\rho}] < 0 \tag{25}$$

or

$$k(\rho) \doteq [\rho - 1 + \ln(2\rho - 1)\frac{1-2\rho}{2\rho}] < 0 \tag{26}$$

and it is seen in Figure (1) that the condition is never satisfied for $\rho > 1$, meaning that the dimorphic solution can be invaded by all nearby phenotypes. This result is also known by biologists who suggest that the end result of this property might be a population with a continuum of phenotypes [5,6,7,8].

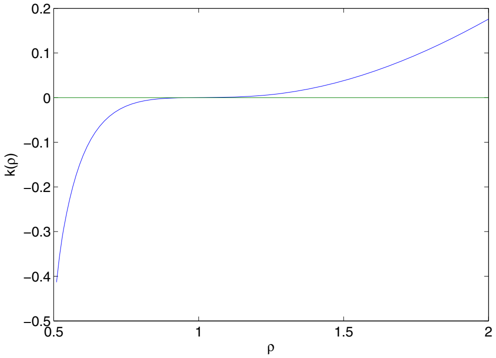

Fig. 1. Curvature of critical branching dimorphism as a function of $\rho = \left(\frac{\sigma_K}{\sigma_C}\right)^2$. Since $k(\rho) > 0$ for all $\rho > 1$, the dimorphism is always invadable.

This result implies that no evolutionarily stable coalitions with more than one phenotype can exist.

5 Quadratic Carrying Capacity: Stable Coexistence

To conclude, we show that if instead of Gaussian, the carrying capacity is a quadratic function

$$K(x) = \begin{cases} K_0(1 - (\frac{x}{a})^2), & |x| \le a \\ 0, & |x| > a \end{cases} \tag{27}$$

where a is a measure of the region of parameter space where the capacity is nonzero, that there can be a bifurcation in which an uninvadable monomorphism loses stability as an uninvadable dimorphism branches from the monomorphic critical point. Since the quadratic function is identical to a Gaussian at quadratic order near the critical point when $\frac{a}{\sqrt{2}}$ is identified with σ_K, it is interesting that the details of the functions away from the bifurcation point can result in such different evolutionary behavior.

For the quadratic carrying capacity, the critical point is again $x^* = 0$, and the curvature condition 17 becomes

$$\sigma_C > \frac{a}{\sqrt{2}} \tag{28}$$

so we again obtain the result that the critical monomorphism is uninvadable for sufficiently large variance of the competition function σ_C.

Turning to the symmetric dimorphism, the criticality condition for the phenotype of the dimorphism 19 becomes

$$\frac{2\frac{\sigma_C^2}{a^2}}{1-\frac{x}{a}^2} = 1 - \tanh\,(\frac{x}{\sigma_C})^2. \tag{29}$$

Since the left side of 29 for $x < a$ has a minimum at $x = 0$, while the right hand side has a maximum at $x = 0$, it is obvious that solutions to this equation for $x < a$ must bifurcate off the origin as σ_C decreases. The curves achieve tangency at $x = 0$ when $\sigma_C = \frac{a}{\sqrt(2)}$, so that a critical symmetric dimorphism begins to exist exactly when the critical monomorphism at $x^* = 0$ becomes invadable, just as in the case of Gaussian carrying capacity. See figure 2

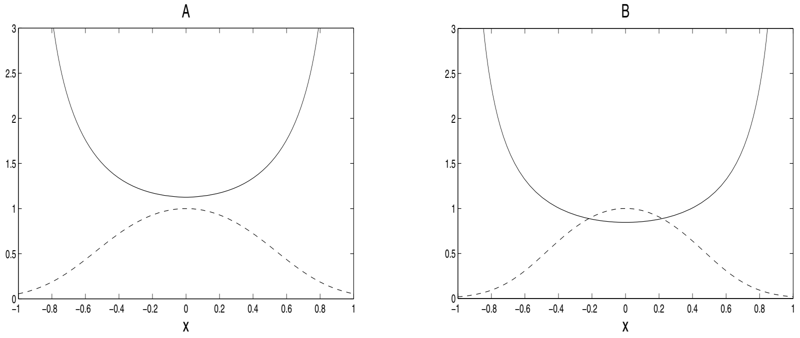

Fig. 2. The left hand side (*solid curve*) and right hand side (*dashed curve*) of 29 for $a = 1$. Figure A is for $\sigma_C = .65$ and Figure B is for $\sigma_C = .75$.

The curvature condition for uninvadability of the critical dimorphism 20 becomes

$$1 - \frac{2\sigma_C^2}{a^2} - \frac{5x^2}{a^2} < 0, \tag{30}$$

and unlike the case of Gaussian carrying capacity, the condition 30 does hold on the critical symmetric dimorphism for values of σ_C less than the critical value $\frac{a}{\sqrt{2}}$, so that in this case, the population does exhibit an uninvadable dimorphism. See Figure 20

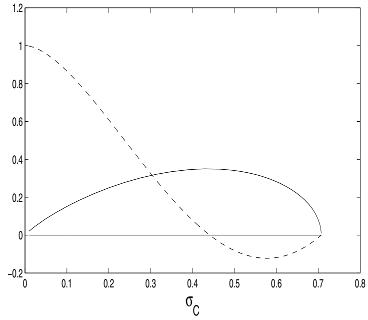

Fig. 3. The value of x^* (*solid curve*) and the curvature condition 30 (*dashed curve* plotted against σ_C

An interesting feature of Figure 3 is that the critical dimorphism becomes invadable around $\sigma_C = 0.4410$ which also is where the critical nonzero phenotype x^* achieves its maximum value. This suggests that the branching process will continue as σ_C continues to decrease with uninvadable coalitions with more and more phenotypes present as the competition between nearby phenotypes becomes weaker. The analysis becomes somewhat more complicated since there is not obvious what kind of coalition might replace the dimorphism when it becomes invadable. For example, the critical dimorphism could split into a four-phenotype population if a branching process similar to that shown in Figure 2 occurs. On the other hand, a non-local bifurcation could result in a trimorphic coalition including possibly the a phenotype with $x = 0$. This will be investigated in future work.

6 Discussion

The fact that such different evolutionary behavior is exhibited by carrying capacity functions that are so similar near the critical point is unexpected. Most likely, there is something degenerate about the case of Gaussian competition in combination with Gaussian carrying capacity that prevents an univadable dimorphic coalition from emerging when an uninvadable dimorphism loses uninvadability. Therefore, it is possible that the speculation that a real population would approach a continuous distribution of phenotypes may not be accurate. The mathematically generic behavior of branching processes suggest that symmetry breaking cascades may be the mechanism by which multi-phenotype populations arise in real populations.

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