

The Mathematics of Resource Allocation in Population Biology. I. Interspecific Competition*

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ABSTRACT

Frequency- and density-dependent selection models in the case of interspecific competition are studied. Several definitions of Evolutionary Stability (ES) and sufficient conditions for ES are proposed. The stability of phenotypic equilibria is studied using the center manifold theory and an appropriate coupling of dynamic equations.

1. INTRODUCTION

Resources in natural populations have been studied from many perspectives: competition for resources in density-dependent selection models (see, e.g., [16, 21, 18]), animal conflicts and *evolutionarily stable strategies* (ESS) in frequency-dependent selection models [20, 19], and resource allocation to male and female functions in sexual populations [15, 3].

The mathematics of ESS theory has been developed by Taylor and Jonker [22], Zeeman [25], Hines [8], Akin [1], Hofbauer et al. [9], Thomas [23], Lessard [12], and Cressman [4], among others, while sex allocation has been treated rigorously by Eshel [6], Uyenoyama and Bengtsson [24], Eshel and Feldman [7], Karlin and Lessard [10, 11], and Lessard [13, 14]. More recently, Cressman [5] extended ESS theory to include density-dependent effects.

From the original definition, an ESS is a *mixed strategy* (a frequency vector with a given number of components, each component being the probability of using some *pure strategy* or behavior) that is uninvadable once

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adopted by all members of a population. Most further works have consisted in trying to establish the evolutionary stability of a population in which the *mean strategy* corresponds to an ESS. *Evolutionary stability* (ES) is understood as stability against perturbations caused by mutations within a given framework, here a strategy set. One of the main difficulties comes from the fact that a whole equilibrium manifold associated with a mean strategy in a population, that is, a *phenotypic equilibrium manifold*, may correspond to an ESS. This happens, for instance, when there are more types of individuals (or genotypes) than pure strategies. Another difficulty arises when strategies are replaced by *resource allocation vectors* (that is, nonnegative vectors) and density-dependent selection is added to frequency-dependent selection, not to mention sex-differentiated selection, since then the original definition of an ESS must be extended.

In this paper, we study frequency- and density-dependent selection models in the case of interspecific competition. Several definitions of evolutionary stability (ES) and sufficient conditions for it are given. In particular, a statement in [8] is rectified. The stability of phenotypic equilibria is studied using the center manifold theory (see, e.g., [17, 2]) as in Cressman [4, 5] but in a way that gives more general results by an appropriate coupling of dynamic equations.

2. GENERAL FORMULATION

2.1. Description of the Model and Some Definitions

Consider a population with n types of individuals. A type may correspond to an allele or a species. Let x_i be the *density of type i* in the population ($i = 1, \dots, n$). Then $x_i \geq 0$ for all i (but not all 0), and $\mathbf{x} = (x_1, \dots, x_n)$ represents the *population state*. Now denote $F_i(\mathbf{x})$ the instantaneous *growth rate* of type i when the population state is \mathbf{x} ($i = 1, \dots, n$). Then the dynamic equations for x_1, \dots, x_n are

$$\dot{x}_i = x_i F_i(\mathbf{x}), \quad i = 1, \dots, n,$$

or, in vector notation,

$$\dot{\mathbf{x}} = \mathbf{x} \cdot \mathbf{F}(\mathbf{x}), \quad (2.1)$$

where \cdot denotes the *Schur product*, that is, the product component by component, and $\mathbf{F}(\mathbf{x}) = (F_1(\mathbf{x}), \dots, F_n(\mathbf{x}))$ is the *growth rate function*. Note that the *population density* $N = \sum_{i=1}^n x_i > 0$ and the *type frequencies* $p_i =$

x_i/N for $i = 1, \dots, n$ satisfy

$$\dot{p}_i = p_i [F_i(N\mathbf{p}) - \langle \mathbf{p}, \mathbf{F}(N\mathbf{p}) \rangle] \quad \text{for } i = 1, \dots, n, \quad (2.2a)$$

and

$$\dot{N} = N \langle \mathbf{p}, \mathbf{F}(N\mathbf{p}) \rangle, \quad (2.2b)$$

where $\langle \circ, \circ \rangle$ denotes the *usual scalar product*, which is the sum of the products component by component, and $\mathbf{p} = \mathbf{x}/N$. If $\mathbf{F}(N\mathbf{p})$ depends only on \mathbf{p} , then we have a *pure frequency-dependent selection model*, while if $\mathbf{F}(N\mathbf{p})$ depends only on N , then we have a *pure density-dependent selection model*. In general, we have a *frequency- and density-dependent selection model*.

A *polymorphic equilibrium* or *interior equilibrium* \mathbf{x}^* of (2.1) is a population state \mathbf{x}^* with all positive components ($x_i^* > 0$ for $i = 1, \dots, n$) satisfying $\mathbf{F}(\mathbf{x}^*) = \mathbf{0}$ ($F_i(\mathbf{x}^*) = 0$ for $i = 1, \dots, n$). At a polymorphic equilibrium \mathbf{x}^* , all types are represented and have a growth rate equal to 0.

Writing $\mathbf{x} = \mathbf{x}^* + \xi$ for ξ small so that \mathbf{x} is a small perturbation of a polymorphic equilibrium \mathbf{x}^* , we have

$$\dot{\xi} = \mathbf{x}^* \cdot d\mathbf{F}(\mathbf{x}^*)\xi + \text{higher order terms} \quad (2.3)$$

where $d\mathbf{F}(\mathbf{x}^*)$ represents the differential of \mathbf{F} at \mathbf{x}^* , that is,

$$d\mathbf{F}(\mathbf{x}^*) = \left\| \left\| \frac{\partial F_i}{\partial x_j}(\mathbf{x}^*) \right\| \right\|_{i,j=1}^n.$$

Note that (2.3) can be written in the form

$$\dot{\xi} = D_{\mathbf{x}^*} d\mathbf{F}(\mathbf{x}^*)\xi + \text{higher order terms}$$

where $D_{\mathbf{x}^*}$ stands for the diagonal matrix with \mathbf{x}^* on the diagonal.

The polymorphic equilibrium \mathbf{x}^* is *stable at a geometric rate* if all eigenvalues of $D_{\mathbf{x}^*} d\mathbf{F}(\mathbf{x}^*)$ have negative real parts; it is *unstable at a geometric rate* if at least one eigenvalue of $D_{\mathbf{x}^*} d\mathbf{F}(\mathbf{x}^*)$ has a positive real part. We are interested in conditions that ensure stability at a geometric rate or at least preclude instability at a geometric rate. In the former case, we will say that \mathbf{x}^* is *strongly evolutionarily stable* (SES), in the latter, *potentially*

evolutionarily stable (PES). If x^* is PES and belongs to an *equilibrium manifold* \mathcal{E} of dimension ≥ 1 whose tangent space at x^* coincides with the generalized eigenspace associated with the eigenvalues of $D_{x^*}dF(x^*)$ having null real parts, then we will say that the equilibrium point x^* is *weakly evolutionarily stable* (WES) and the equilibrium manifold \mathcal{E} *locally evolutionarily stable* (LES) at x^* .

In general, for any *admissible equilibrium* x^* of (2.1), that is, any x^* satisfying $x_i^* \geq 0$ for $i = 1, \dots, n$ and $F_i(x^*) = 0$ if $x_i^* > 0$ such that the growth rates of all types represented at equilibrium are 0, we have

$$\dot{\xi} = [D_{x^*}dF(x^*) + D_{F(x^*)}] \xi + \text{higher order terms} \quad (2.4)$$

where $\xi = x - x^*$. If $x_i^* = 0$ for all i , then x^* is a *polymorphic equilibrium*. If $x_i^* = 0$ for some i , then x^* is a *boundary equilibrium*.

For any *admissible equilibrium* x^* , the eigenvalues in the linear approximation of (2.4) are the quantities

$$F_i(x^*) \quad \text{for which} \quad x_i^* = 0,$$

that is, the growth rates of all types not represented at equilibrium, and the eigenvalues of $D_{x^*}dF(x^*)$ on the closed subspace

$$\mathcal{S}^+ = \{ \xi = (\xi_1, \dots, \xi_n) : \xi_i = 0 \text{ if } x_i^* = 0 \}$$

for perturbations affecting only the densities of types represented at equilibrium. If the latter eigenvalues have all real parts ≤ 0 (< 0), then x^* is *internally PES* (*internally SES*). If the former eigenvalues are all ≤ 0 (< 0), then x^* is *externally PES* (*externally SES*). If all the eigenvalues have real parts ≤ 0 (< 0), then x^* is PES (SES). For a *polymorphic equilibrium*, PES (SES) is equivalent to internally PES (internally SES). In general, if the generalized eigenspace associated with the eigenvalues having null real parts is of dimension ≥ 1 and coincides with the tangent space of an equilibrium manifold \mathcal{E} at x^* , then x^* is WES and \mathcal{E} is LES at x^* .

2.2. Stability Conditions

Let us consider the following conditions:

CONDITION I. $dF(x^*)$ is negative semidefinite with respect to the usual scalar product $\langle \circ, \circ \rangle$, or simply, negative semidefinite, in the sense that $\langle \xi, dF(x^*) \xi \rangle \leq 0$ for all ξ .

CONDITION I'. $dF(x^*)$ is negative definite with respect to $\langle \circ, \circ \rangle$, or simply, negative definite, in the sense that we have Condition I with equality only if $\xi = 0$.

CONDITION II. $QdF(x^*)$ is negative semidefinite with respect to the scalar product $\langle \circ, \circ \rangle_Q = \langle \circ, Q^{-1} \circ \rangle$, where Q^{-1} is the inverse of Q , for all Q symmetric positive definite with respect to $\langle \circ, \circ \rangle$, that is, Q satisfying $\langle \xi, Q\eta \rangle = \langle Q\xi, \eta \rangle$ for all ξ, η and $\langle \xi, Q\xi \rangle \geq 0$ for all ξ with equality only if $\xi = 0$. (In such a case, the scalar product $\langle \circ, \circ \rangle_Q$ is well defined, since Q^{-1} is symmetric positive definite.)

CONDITION II'. $QdF(x^*)$ is negative definite with respect to $\langle \circ, \circ \rangle_Q$ in Condition II.

CONDITION III. $QdF(x^*)$ has only eigenvalues with nonpositive real parts for all Q symmetric positive semidefinite.

CONDITION III'. $QdF(x^*)$ has only eigenvalues with negative real parts for all Q symmetric positive definite.

Condition I implies Condition II, since for all Q symmetric positive definite we have

$$\langle \xi, QdF(x^*) \xi \rangle_Q = \langle \xi, dF(x^*) \xi \rangle \leq 0 \quad \text{for all } \xi \quad (2.5)$$

if Condition I holds. But then all eigenvalues of $QdF(x^*)$ have nonpositive real parts: if λ is an eigenvalue, then there exist real vectors φ and ψ , not both equal to 0 , satisfying

$$QdF(x^*) \varphi = \text{Re } \lambda \varphi - \text{Im } \lambda \psi,$$

$$QdF(x^*) \psi = \text{Re } \lambda \psi + \text{Im } \lambda \varphi,$$

and for these vectors, (2.5) implies

$$\operatorname{Re} \lambda \langle \varphi, \varphi \rangle - \operatorname{Im} \lambda \langle \varphi, \psi \rangle \leq 0, \quad (2.6a)$$

$$\operatorname{Re} \lambda \langle \psi, \psi \rangle + \operatorname{Im} \lambda \langle \psi, \varphi \rangle \leq 0, \quad (2.6b)$$

which entails by summation

$$\operatorname{Re} \lambda (\langle \varphi, \varphi \rangle + \langle \psi, \psi \rangle) \leq 0, \quad (2.7)$$

and therefore

$$\operatorname{Re} \lambda \leq 0, \quad (2.8)$$

since $\langle \varphi, \varphi \rangle + \langle \psi, \psi \rangle > 0$. We also conclude by continuity that $QdF(x^*)$ has only eigenvalues with nonpositive real parts for all Q symmetric positive semidefinite (take $Q + \varepsilon I$ with I the identity, and let $\varepsilon \rightarrow 0$).

Conversely, if we assume Condition III, we can take $Q = \xi \xi^T$ (T for transpose) to conclude that the real parts of all eigenvalues of $QdF(x^*)$, in particular $\langle \xi, dF(x^*)\xi \rangle$ with right eigenvector ξ , are nonpositive.

Assuming Condition I', we have a strict inequality in (2.5) for all $\xi \neq 0$, which compels a strict inequality somewhere in (2.6a, b) and consequently a strict inequality in (2.7) and (2.8).

To sum up, we have the following result, which can be traced back for the main part to Hines [8]:

LEMMA 1. *Conditions I, I', II, II', III, III' are related by the implications*

$$\begin{array}{ccccc} \text{I} & \Leftrightarrow & \text{II} & \Leftrightarrow & \text{III} \\ \uparrow & & \uparrow & & \uparrow \\ \text{I}' & \Leftrightarrow & \text{II}' & \Rightarrow & \text{III}' \end{array}$$

REMARK 1 ON LEMMA 1. Hines [8] proved $\text{I}' \Leftrightarrow \text{III}'$. But $\text{III}' \Rightarrow \text{I}'$ is false. A counterexample is provided by

$$dF(x^*) = \begin{bmatrix} -\frac{1}{2} & -1 \\ 0 & -\frac{1}{2} \end{bmatrix}.$$

For $\xi = (\xi_1, \xi_2)$, we have

$$\langle \xi, dF(x^*) \xi \rangle = -\frac{1}{2}(\xi_1 + \xi_2)^2 \leq 0$$

with equality only if $\xi_1 + \xi_2 = 0$, and therefore $dF(x^*)$ is negative semidefinite but not negative definite. Nevertheless, given any matrix

$$Q = \begin{bmatrix} a & b \\ b & c \end{bmatrix}$$

positive definite, that is, with $a > 0$, $c > 0$, $ac - b^2 > 0$, the eigenvalues of

$$QdF(x^*) = \begin{bmatrix} -\frac{a}{2} & -a - \frac{b}{2} \\ \frac{b}{2} & -b - \frac{c}{2} \end{bmatrix}$$

have negative real parts, since

$$\det[QdF(x^*) - \lambda I] = \lambda^2 + a_1\lambda + a_2$$

has

$$a_1 = b + \frac{c+a}{2} \geq b + \sqrt{ac} > b + |b| \geq 0,$$

$$a_2 = \frac{ac - b^2}{4} > 0.$$

Hines's proof used properties of the trace of a matrix and the claim that $\langle \xi, dF(x^*) \xi \rangle = 0$ for some $\xi \neq 0$ is precluded in the case $dF(x^*)$ nonsingular. This claim is false, as illustrated above.

REMARK 2 ON LEMMA 1. In the case $dF(x^*)$ symmetric, that is, symmetric with respect to $\langle \circ, \circ \rangle$, we have $III' \Rightarrow I'$. Moreover, in such a case, Condition III' (III) has only to hold for some Q symmetric positive definite to imply Condition I' (I). For $QdF(x^*)$ is then symmetric with respect to $\langle \circ, \circ \rangle_Q$ and negative definite (semidefinite) with respect to the same scalar

product if and only if all the eigenvalues of $QdF(x^*)$, which are necessarily real, are negative (nonpositive). In such a case, $dF(x^*)$ is negative definite (semidefinite) owing to (2.5).

REMARK 3 ON LEMMA 1. A more refined statement of I' (I) \Rightarrow III' (III) is:

$QdF(x^)$ has only eigenvalues with negative (nonpositive) real parts on a closed subspace \mathcal{S} , that is, $QdF(x^*)\xi$ belongs to \mathcal{S} if ξ belongs to \mathcal{S} , if Q is symmetric positive definite and $dF(x^*)$ negative definite (semidefinite) on \mathcal{S} .*

2.3. Stability of Polymorphic Equilibria

A direct consequence of Lemma 1 is:

RESULT 1. *A polymorphic equilibrium x^* of (2.1) is strongly evolutionarily stable (SES) if $dF(x^*)$ is negative definite (Condition I), and at least potentially evolutionarily stable (PES) if $dF(x^*)$ is negative semidefinite (Condition I).*

REMARK ON RESULT 1. Actually it is sufficient that $dF(x^*)$ be negative definite (semidefinite, respectively) with respect to $\langle \circ, \circ \rangle_D$ where D is some positive diagonal matrix (a diagonal matrix with all positive entries on the main diagonal), since then $dF(x^*) = DD^{-1}dF(x^*)$ and $D^{-1}dF(x^*)$ is negative definite (semidefinite, respectively) with respect to $\langle \circ, \circ \rangle$, so that all the eigenvalues of

$$D_{x^*}dF(x^*) = (D_{x^*}D)[D^{-1}dF(x^*)] \quad (2.9)$$

have negative (nonpositive, respectively) real parts by Lemma 1.

EXAMPLE. The Lotka-Volterra competition model assumes near equilibrium (see, e.g., [16, 21])

$$F_i(x) = c_i \left[k_i - \sum_{j=1}^n \alpha_{ij} x_j \right] \quad \text{for } i = 1, \dots, n, \quad (2.10)$$

where $c_i > 0$, $k_i > 0$, and $\alpha_{ij} \geq 0$ for $i, j = 1, \dots, n$. The terms in square brackets on the right side of (2.10) can be viewed as the first terms in a

Taylor series of $F_i(\mathbf{x})$ near equilibrium. The differential of $\mathbf{F}(\mathbf{x}) = (F_1(\mathbf{x}), \dots, F_n(\mathbf{x}))$ is

$$d\mathbf{F}(\mathbf{x}) = \|\| -c_i \alpha_{ij} \|\|_{i,j=1}^n. \tag{2.11}$$

Therefore, $d\mathbf{F}(\mathbf{x})$ is negative definite (semidefinite) with respect to $\langle \circ, \circ \rangle_D$, where $\mathbf{c} = (c_1, \dots, c_n)$, if and only if the matrix $\|\| \alpha_{ij} \|\|_{i,j=1}^n$ is positive definite (semidefinite) with respect to the usual scalar product. This matrix has been called the *competition matrix*.

2.4. Stability of Boundary Equilibria

From Remark 3 on Lemma 1, we conclude:

RESULT 2. A boundary equilibrium \mathbf{x}^* of (2.1) is SES (PES) if $d\mathbf{F}(\mathbf{x}^*)$ is negative definite (semidefinite) on the subspace \mathcal{S}^+ corresponding to the positive components of \mathbf{x}^* and $F_i(\mathbf{x}^*) < 0$ (≤ 0) for all i such that $x_i^* = 0$.

As in Result 1, it is sufficient that $d\mathbf{F}(\mathbf{x}^*)$ be negative definite (semidefinite) on \mathcal{S}^+ with respect to $\langle \circ, \circ \rangle_D$ for some positive diagonal matrix D .

2.5. Case of Pure Frequency Dependence

Consider the system of equations (2.2a) in the case $F_i(N\mathbf{p}) = F_i(\mathbf{p})$ for $i = 1, \dots, n$ and $\mathbf{p} = (p_1, \dots, p_n)$ satisfying $\sum_{i=1}^n p_i = 1$ with $p_i \geq 0$ for $i = 1, \dots, n$. According to Result 1, a polymorphic equilibrium \mathbf{p}^* is SES (PES) if

$$d\mathbf{F}(\mathbf{p}^*) - U D_{\mathbf{p}^*} d\mathbf{F}(\mathbf{p}^*), \tag{2.12}$$

where U is the unit matrix (a matrix with all entries equal to 1), is negative definite (semidefinite) on

$$\mathcal{S}_\perp = \left\{ \boldsymbol{\xi} = (\xi_1, \dots, \xi_n) : \sum_{i=1}^n \xi_i = 0 \right\}, \tag{2.13}$$

which is the same as $d\mathbf{F}(\mathbf{p}^*)$ negative definite (semidefinite) on \mathcal{S}_\perp . For a boundary equilibrium \mathbf{p}^* , Result 2 gives the following conditions: $d\mathbf{F}(\mathbf{p}^*)$ negative definite (semidefinite) on

$$\mathcal{S}_\perp^+ = \left\{ \boldsymbol{\xi} = (\xi_1, \dots, \xi_n) : \sum_{i=1}^n \xi_i = 0, \xi_i = 0 \text{ whenever } p_i^* = 0 \right\}, \tag{2.14}$$

and

$$F_i(\mathbf{p}^*) - \langle \mathbf{p}^*, \mathbf{F}(\mathbf{p}^*) \rangle < 0 \ (\leq 0) \quad \text{whenever } p_i^* = 0, \quad (2.15)$$

while the equilibrium condition is

$$F_i(\mathbf{p}^*) - \langle \mathbf{p}^*, \mathbf{F}(\mathbf{p}^*) \rangle = 0 \quad \text{whenever } p_i^* > 0. \quad (2.16)$$

These two conditions are equivalent to

$$\langle \mathbf{p}^*, \mathbf{F}(\mathbf{p}) \rangle \geq \langle \mathbf{p}, \mathbf{F}(\mathbf{p}) \rangle \quad (2.17)$$

for all \mathbf{p} close enough to \mathbf{p}^* , with equality if and only if $\mathbf{p} = \mathbf{p}^*$. As a matter of fact, we have under the equilibrium condition

$$\begin{aligned} \langle \mathbf{p} - \mathbf{p}^*, \mathbf{F}(\mathbf{p}) \rangle &= \langle \mathbf{p} - \mathbf{p}^*, \mathbf{F}(\mathbf{p}^*) \rangle + \langle \mathbf{p} - \mathbf{p}^*, d\mathbf{F}(\mathbf{p}^*)(\mathbf{p} - \mathbf{p}^*) \rangle \\ &\quad + \text{higher order terms} \\ &= \sum_{i: p_i^* = 0} (p_i - p_i^*) F_i(\mathbf{p}^*) + \sum_{i: p_i^* > 0} (p_i - p_i^*) \langle \mathbf{p}^*, \mathbf{F}(\mathbf{p}^*) \rangle \\ &\quad + \langle \mathbf{p} - \mathbf{p}^*, d\mathbf{F}(\mathbf{p}^*)(\mathbf{p} - \mathbf{p}^*) \rangle \\ &\quad + \text{higher order terms} \\ &= \sum_{i: p_i^* = 0} (p_i - p_i^*) [F_i(\mathbf{p}^*) - \langle \mathbf{p}^*, \mathbf{F}(\mathbf{p}^*) \rangle] \\ &\quad + \langle \mathbf{p} - \mathbf{p}^*, d\mathbf{F}(\mathbf{p}^*)(\mathbf{p} - \mathbf{p}^*) \rangle \\ &\quad + \text{higher order terms,} \end{aligned} \quad (2.18)$$

and the equivalence immediately ensues. The condition (2.17) is known as the ESS condition [20, 22, 9].

2.6. Case of Pure Density Dependence

In the case of pure density dependence, we have the equations (2.2a, b) with $\mathbf{F}(N\mathbf{p}) = \mathbf{f}(N)$ for all $N > 0$ and all $\mathbf{p} = (p_1, \dots, p_n)$ with $\sum_{i=1}^n p_i = 1$, $p_i \geq 0$ for $i = 1, \dots, n$. Near a polymorphic equilibrium (\mathbf{p}^*, N^*) such that

$$p_i^* > 0 \text{ and } f_i(N^*) = \langle \mathbf{p}^*, \mathbf{f}(N^*) \rangle = 0 \quad \text{for } i = 1, \dots, n,$$

we have

$$\begin{bmatrix} \dot{\mathbf{p}} - \dot{\mathbf{p}}^* \\ N - N^* \end{bmatrix} = \begin{bmatrix} O & D_{\mathbf{p}^*}\{df(N^*) - \langle \mathbf{p}^*, df(N^*) \rangle \mathbf{u} \} \\ O & N^* \langle \mathbf{p}^*, df(N^*) \rangle \end{bmatrix} \begin{bmatrix} \mathbf{p} - \mathbf{p}^* \\ N - N^* \end{bmatrix} + \text{higher order terms}, \tag{2.19}$$

where O denotes a zero matrix (a matrix with all entries equal to 0), \mathbf{u} a unit vector (a vector with all components equal to 1), and

$$df(N^*) = \begin{bmatrix} \frac{df_1}{dN}(N^*) \\ \vdots \\ \frac{df_n}{dN}(N^*) \end{bmatrix}.$$

If

$$\langle \mathbf{p}^*, df(N^*) \rangle < 0, \tag{2.20}$$

then the equilibrium (\mathbf{p}^*, N^*) is PES. Actually, owing to the center manifold theory (see, e.g., [17, 2]), the equilibrium manifold \mathcal{E}^* characterized by $N = N^*$ is locally evolutionarily stable (LES) at (\mathbf{p}^*, N^*) in the sense that there will be convergence to a nearby equilibrium point (\mathbf{p}, N^*) belonging to \mathcal{E}^* from any point near (\mathbf{p}, N^*) . Finally, if

$$df(N^*) < 0,$$

that is,

$$\frac{df_i}{dN}(N^*) < 0 \quad \text{for } i = 1, \dots, n,$$

then \mathcal{E}^* is LES at every polymorphic equilibrium (\mathbf{p}^*, N^*) belonging to \mathcal{E}^* .

For a boundary equilibrium (\mathbf{p}^*, N^*) , we can relabel the types if necessary so that

$$\mathbf{p}^* = (\mathbf{p}_1^*, \mathbf{p}_2^*) \tag{2.21}$$

with

$$\mathbf{p}_1^* = (p_1^*, \dots, p_k^*),$$

$$\mathbf{p}_2^* = (p_{k+1}^*, \dots, p_n^*) = (0, \dots, 0),$$

and

$$\mathbf{f}(N^*) = (\mathbf{f}_1(N^*), \mathbf{f}_2(N^*)) \quad (2.22)$$

with

$$\mathbf{f}_1(N^*) = (f_1(N^*), \dots, f_k(N^*)) = (0, \dots, 0),$$

$$\mathbf{f}_2(N^*) = (f_{k+1}(N^*), \dots, f_n(N^*)),$$

where $f_{k+1}(N^*) \neq 0, \dots, f_n(N^*) \neq 0$. Near the equilibrium we have

$$\begin{bmatrix} \dot{\mathbf{p}}_1 - \mathbf{p}_1^* \\ \dot{\mathbf{p}}_2 - \mathbf{p}_2^* \\ \dot{N} - N^* \end{bmatrix} = \begin{bmatrix} O & A & B \\ O & D & O \\ O & C & E \end{bmatrix} \begin{bmatrix} \mathbf{p}_1 - \mathbf{p}_1^* \\ \mathbf{p}_2 - \mathbf{p}_2^* \\ N - N^* \end{bmatrix}$$

+ higher order terms, (2.23)

where

$$A = -D_{\mathbf{p}_1^*} U D_{\mathbf{f}_2(N^*)}, \quad B = D_{\mathbf{p}_1^*} \{ d\mathbf{f}_1(N^*) - \langle \mathbf{p}_1^*, d\mathbf{f}_1(N^*) \rangle \mathbf{u} \}$$

$$D = D_{\mathbf{f}_2(N^*)},$$

$$C = N^* \mathbf{f}_2(N^*)^T, \quad E = N^* \langle \mathbf{p}_1^*, d\mathbf{f}_1(N^*) \rangle$$

(T for transpose). Apart from 0, the eigenvalues of the matrix in (2.23) are

$$f_{k+1}(N^*), \dots, f_n(N^*) \quad \text{and} \quad N^* \langle \mathbf{p}_1^*, d\mathbf{f}_1(N^*) \rangle. \quad (2.24)$$

If these quantities are all negative, which will be necessarily the case if

$$f_{k+1}(N^*) < 0, \dots, \quad f_n(N^*) < 0, \quad \frac{df_1}{dN}(N^*) < 0, \dots, \quad \frac{df_k}{dN}(N^*) < 0,$$

then the equilibrium point (\mathbf{p}^*, N^*) is PES, and the equilibrium manifold \mathcal{E}^* to which it belongs, characterized by

$$N = N^* \tag{2.25a}$$

and

$$p_i \geq 0 \quad \text{with equality if } f_i(N^*) \neq 0, \quad i = 1, \dots, n, \tag{2.25b}$$

is LES at (\mathbf{p}^*, N^*)

3. RESOURCE ALLOCATION AND INTERSPECIFIC COMPETITION

3.1. Dynamical Equation for Resource Allocation

Assume that type i corresponds to a species characterized by some resource allocation vector $\mathbf{R}_i = (R_i^{(1)}, \dots, R_i^{(m)})$, where $R_i^{(k)} \geq 0$ (> 0 for some k) represents the quantity of resources allocated to a function or activity k ($k = 1, \dots, m$ and $i = 1, \dots, n$). The total resource allocation vector in a population in state $\mathbf{x} = (x_1, \dots, x_n)$, where $x_i \geq 0$ represents the density of species i ($i = 1, \dots, n$) and $\sum_{i=1}^n x_i = N$, is

$$\mathbf{R} = \sum_{i=1}^n x_i \mathbf{R}_i, \tag{3.1}$$

whose components are denoted $R^{(1)}, \dots, R^{(m)}$. Now suppose that the growth rate of type i ($i = 1, \dots, n$) is in the form

$$\begin{aligned} F_i(\mathbf{x}) &= \mathbf{R}_i^T \mathbf{G}(\mathbf{R}) \quad (T \text{ for transpose}) \\ &= \sum_{k=1}^m R_i^{(k)} G^{(k)}(\mathbf{R}), \end{aligned} \tag{3.2}$$

where the k th component of $\mathbf{G}(\mathbf{R})$, $G^{(k)}(\mathbf{R})$, represents the growth rate per unit of resources allocated to a function k when the total resource allocation vector in the population is \mathbf{R} ($k = 1, \dots, m$). The function $\mathbf{G}(\mathbf{R})$ is the *growth rate function per unit of resources*.

Since the growth rates depend only on \mathbf{R} , it is convenient to transform the dynamical system of equations (2.1) for \mathbf{x} into a system for (\mathbf{x}, \mathbf{R}) using (3.2) and

$$\dot{\mathbf{R}} = \sum_{i=1}^n \dot{x}_i \mathbf{R}_i. \quad (3.3)$$

We get

$$\dot{x}_i = x_i \mathbf{R}_i^T \mathbf{G}(\mathbf{R}), \quad i = 1, \dots, n, \quad (3.4a)$$

$$\dot{\mathbf{R}} = \sum_{i=1}^n x_i \mathbf{R}_i \mathbf{R}_i^T \mathbf{G}(\mathbf{R}). \quad (3.4b)$$

The relation (3.1) between \mathbf{x} and \mathbf{R} is *invariant* in (3.4a, b) and will be assumed throughout this section.

3.2. Stability of Phenotypic Equilibria

Let $\mathbf{x}^* = (x_1^*, \dots, x_n^*)$ and $\mathbf{R}^* = \sum_{i=1}^n x_i^* \mathbf{R}_i$ be such that $x_i^* > 0$ for $i = 1, \dots, n$ and $\mathbf{G}(\mathbf{R}^*) = \mathbf{0}$. Then $(\mathbf{x}^*, \mathbf{R}^*)$ is said to be a *polymorphic phenotypic equilibrium* of (3.4a, b). Note that $(\mathbf{x}^*, \mathbf{R}^*)$ belongs to a *phenotypic equilibrium manifold*

$$\mathcal{M}^* = \left\{ (\mathbf{x}, \mathbf{R}^*): \sum_{i=1}^n x_i \mathbf{R}_i = \mathbf{R}^*, x_i \geq 0 \text{ for } i = 1, \dots, n \right\}. \quad (3.5)$$

Writing

$$x_i = x_i^* + \xi_i, \quad i = 1, \dots, n, \quad (3.6a)$$

$$\mathbf{R} = \sum_{i=1}^n (x_i^* + \xi_i) \mathbf{R}_i = \mathbf{R}^* + \boldsymbol{\zeta}, \quad (3.6b)$$

we have

$$\dot{\xi}_i = x_i^* \mathbf{R}_i^T d\mathbf{G}(\mathbf{R}^*) \boldsymbol{\zeta} + \text{higher order terms}, \quad i = 1, \dots, n, \quad (3.7a)$$

$$\dot{\boldsymbol{\zeta}} = Q(\mathbf{x}^*) d\mathbf{C}(\mathbf{R}^*) \boldsymbol{\zeta} + \text{higher order terms}, \quad (3.7b)$$

where

$$Q(\mathbf{x}^*) = \sum_{i=1}^n x_i^* \mathbf{R}_i \mathbf{R}_i^T \tag{3.8}$$

and

$$d\mathbf{G}(\mathbf{R}^*) = \left\| \frac{\partial \mathbf{G}^{(k)}}{\partial R^{(l)}}(\mathbf{R}^*) \right\|_{k,l=1}^m. \tag{3.9}$$

Let \mathcal{S} denote the space engendered by $\mathbf{R}_1, \dots, \mathbf{R}_n$, that is,

$$\mathcal{S} = \left\{ \zeta = \sum_{i=1}^n \xi_i \mathbf{R}_i : \xi_i \text{ real for } i = 1, \dots, n \right\}. \tag{3.10}$$

\mathcal{S} is the space engendered by the resource allocation vectors. Note that $Q(\mathbf{x}^*)d\mathbf{G}(\mathbf{R}^*)$ is closed on \mathcal{S} [take $t\zeta$ in (3.7b), let $t \rightarrow 0$, and use the invariance of (3.1)]. Moreover, $Q(\mathbf{x}^*)$ is symmetric and positive definite on \mathcal{S} , since

$$\langle \zeta, Q(\mathbf{x}^*)\zeta \rangle = \langle \zeta Q(\mathbf{x}^*), \zeta \rangle = \sum_{i=1}^n x_i^* \langle \zeta, \mathbf{R}_i \rangle^2 \geq 0 \tag{3.11}$$

with equality if and only if $\langle \zeta, \mathbf{R}_i \rangle = 0$ for $i = 1, \dots, n$, which is possible only if $\zeta = 0$ for ζ in \mathcal{S} . Therefore, all eigenvalues of $Q(\mathbf{x}^*)d\mathbf{G}(\mathbf{R}^*)$ on \mathcal{S} will have negative real parts if $d\mathbf{G}(\mathbf{R}^*)$ is negative definite on \mathcal{S} (Remark 3 on Lemma 1). On the other hand, all other eigenvalues in the linear approximation of (3.7a, b) for any $\xi = (\xi_1, \dots, \xi_n)$ small and $\zeta = \sum_{i=1}^n \xi_i \mathbf{R}_i$ are 0, since we have the linear approximation

$$\begin{bmatrix} \dot{\xi} \\ \dot{\zeta} \end{bmatrix} \cong \begin{bmatrix} O & S(\mathbf{x}^*)d\mathbf{G}(\mathbf{R}^*) \\ O & Q(\mathbf{x}^*)d\mathbf{G}(\mathbf{R}^*) \end{bmatrix} \begin{bmatrix} \xi \\ \zeta \end{bmatrix}, \tag{3.12}$$

where O designates a zero matrix, while $S(\mathbf{x}^*)$ is a matrix whose i th row is $x_i^* \mathbf{R}_i^T$ for $i = 1, \dots, n$. We conclude at once:

RESULT 3. *Every polymorphic phenotypic equilibrium $(\mathbf{x}^*, \mathbf{R}^*)$ of (3.4a, b) is PES if $dG(\mathbf{R}^*)$ is negative definite on \mathcal{S} .*

But according to the center manifold theory (see, e.g., [17, 2]), the generalized eigenspace associated with the eigenvalue 0 at $(\mathbf{x}^*, \mathbf{R}^*)$ of Result 3 will be tangent to an invariant manifold passing through $(\mathbf{x}^*, \mathbf{R}^*)$. In the case at hand such an invariant manifold can only be the phenotypic equilibrium manifold corresponding to $\zeta = \mathbf{0}$ in (3.6b), that is, \mathcal{M}^* as defined in (3.5) and characterized by $\mathbf{R} = \mathbf{R}^*$. Moreover, every point in \mathcal{M}^* being an equilibrium, \mathcal{M}^* as a manifold will attract every trajectory of (3.4a, b) starting from (\mathbf{x}, \mathbf{R}) satisfying (3.1) and close enough to $(\mathbf{x}^*, \mathbf{R}^*)$ in the sense that the trajectory will converge to a point on \mathcal{M}^* but not necessarily $(\mathbf{x}^*, \mathbf{R}^*)$. Then we have that \mathcal{M}^* is locally evolutionarily stable (LES) at $(\mathbf{x}^*, \mathbf{R}^*)$.

RESULT 4. *The phenotypic equilibrium manifold \mathcal{M}^* of (3.5) is locally evolutionarily stable (LES) for (3.4a, b) at every polymorphic equilibrium $(\mathbf{x}^*, \mathbf{R}^*)$ of \mathcal{M}^* if $dG(\mathbf{R}^*)$ is negative definite on \mathcal{S} .*

The condition that $(\mathbf{x}^*, \mathbf{R}^*)$ is polymorphic in Result 4 is not necessary in *generic cases*: it suffices that if

$$\sum_{i=1}^n x_i^* \mathbf{R}_i = \mathbf{R}^* \quad \text{with} \quad x_i^* \geq 0 \quad \text{for} \quad i=1, \dots, n \quad (3.13)$$

then

$$\{\mathbf{R}_i : x_i^* > 0\} \quad \text{and} \quad \{\mathbf{R}_i : x_i^* \geq 0\} \quad (3.14)$$

engender the same space \mathcal{S} . This guarantees that $Q(\mathbf{x}^*)$ is positive definite on \mathcal{S} [see (3.11)]. If the above condition defining a generic case is not satisfied, small perturbations on $\mathbf{R}_1, \dots, \mathbf{R}_n$ can make the conditions satisfied. We may also assume, without loss of generality, that \mathcal{S} is the space of all m -dimensional vectors. If this is not the case, we consider an orthonormal basis for \mathcal{S} with all nonnegative basis vectors, which are defined as new functions or activities. All resource allocation vectors are then expressed in this new coordinate system with a number of coordinates equal to the dimension of \mathcal{S} . Defining a phenotypic equilibrium satisfying (3.13) as *admissible*, we have:

RESULT 5. *In generic cases, the phenotypic equilibrium manifold \mathcal{M}^* of (3.5) is LES for (3.4a, b) at every admissible equilibrium $(\mathbf{x}^*, \mathbf{R})$ of \mathcal{M}^* if $d\mathbf{G}(\mathbf{R}^*)$ is negative definite on \mathcal{S} .*

3.3. Stability against the Introduction of a New Function or Activity

The stability of an equilibrium manifold against the introduction of a new function or activity is also of interest. Consider the extended resource allocation vectors

$$\tilde{\mathbf{R}}_i = (R_i^{(1)}, \dots, R_i^{(m)}, R_i^{(m+1)}) \quad \text{for } i = 1, \dots, n + 1,$$

where

$$R_i^{(m+1)} = 0 \quad \text{for } i = 1, \dots, n,$$

$$R_i^{(m+1)} > 0 \quad \text{for } i = n + 1,$$

and the extended growth rate function per unit of resources,

$$\tilde{\mathbf{G}}(\tilde{\mathbf{R}}) = (\tilde{G}^{(1)}(\tilde{\mathbf{R}}), \dots, \tilde{G}^{(m)}(\tilde{\mathbf{R}}), \tilde{G}^{(m+1)}(\tilde{\mathbf{R}})),$$

where

$$\tilde{\mathbf{R}} = (\tilde{R}^{(1)}, \dots, \tilde{R}^{(m)}, \tilde{R}^{(m+1)}) = \sum_{i=1}^{n+1} x_i \tilde{\mathbf{R}}_i$$

is the total resource allocation vector in the population if the density of $\tilde{\mathbf{R}}_i$ is $x_i \geq 0$ for $i = 1, \dots, n + 1$. Let

$$\tilde{\mathbf{x}}^* = (x_1^*, \dots, x_n^*, x_{n+1}^*)$$

and

$$\tilde{\mathbf{R}}^* = (\tilde{R}^{*(1)}, \dots, \tilde{R}^{*(m)}, \tilde{R}^{*(m+1)})$$

$$= \sum_{i=1}^{n+1} x_i^* \tilde{\mathbf{R}}_i = \sum_{i=1}^n x_i^* \tilde{\mathbf{R}}_i$$

be such that

$$x_{n+1}^* = 0$$

and

$$\tilde{G}^{(1)}(\tilde{\mathbf{R}}^*) = \dots = \tilde{G}^{(m)}(\tilde{\mathbf{R}}^*) = 0.$$

Then $(\tilde{\mathbf{x}}^*, \tilde{\mathbf{R}}^*)$ is an admissible phenotypic equilibrium which belongs to the phenotypic equilibrium manifold

$$\tilde{\mathcal{M}}^* = \left\{ (x_1, \dots, x_n, 0, \tilde{\mathbf{R}}^*) : \sum_{i=1}^n x_i \tilde{\mathbf{R}}_i = \tilde{\mathbf{R}}^*, x_i \geq 0 \text{ for } i = 1, \dots, n \right\}.$$

For

$$\begin{aligned} \tilde{\xi} &= (\xi, \xi_{n+1}) = (\xi_1, \dots, \xi_n, \xi_{n+1}) \\ &= (x_1 - x_1^*, \dots, x_n - x_n^*, x_{n+1} - x_{n+1}^*) \end{aligned}$$

and

$$\tilde{\zeta} = \tilde{\mathbf{R}} - \tilde{\mathbf{R}}^* = \sum_{i=1}^{n+1} \xi_i \tilde{\mathbf{R}}_i,$$

we have

$$\begin{aligned} \dot{\xi}_i &= x_i \tilde{\mathbf{R}}_i^T \tilde{\mathbf{G}}(\tilde{\mathbf{R}}), \quad i = 1, \dots, n, \\ \dot{\xi}_{n+1} &= x_{n+1} \tilde{\mathbf{R}}_{n+1}^T \tilde{\mathbf{G}}(\tilde{\mathbf{R}}), \\ \dot{\zeta} &= \sum_{i=1}^{n+1} x_i \tilde{\mathbf{R}}_i \tilde{\mathbf{R}}_i^T \tilde{\mathbf{G}}(\tilde{\mathbf{R}}), \end{aligned}$$

such that near $(\tilde{\mathbf{x}}^*, \tilde{\mathbf{R}}^*)$

$$\begin{bmatrix} \dot{\xi} \\ \dot{\xi}_{n+1} \\ \dot{\zeta} \end{bmatrix} \begin{bmatrix} 0 & 0 & \tilde{S}(\tilde{\mathbf{x}}^*) d\tilde{\mathbf{G}}(\tilde{\mathbf{R}}^*) \\ 0 & \tilde{\mathbf{R}}_{n+1}^T \tilde{\mathbf{G}}(\tilde{\mathbf{R}}^*) & 0 \\ 0 & \tilde{\mathbf{R}}_{n+1} \tilde{\mathbf{R}}_{n+1}^T \tilde{\mathbf{G}}(\tilde{\mathbf{R}}^*) & \tilde{Q}(\tilde{\mathbf{x}}^*) d\tilde{\mathbf{G}}(\tilde{\mathbf{R}}^*) \end{bmatrix} \begin{bmatrix} \xi \\ \xi_{n+1} \\ \zeta \end{bmatrix},$$

where $\tilde{S}(\tilde{x}^*)$ is a matrix whose i th row is $x_i^* \tilde{R}_i^T$ for $i = 1, \dots, n$ and

$$\tilde{Q}(\tilde{x}^*) = \sum_{i=1}^{n+1} x_i^* \tilde{R}_i \tilde{R}_i^T = \sum_{i=1}^n x_i^* \tilde{R}_i \tilde{R}_i^T.$$

Since the last row of $\tilde{Q}(\tilde{x}^*)$ is $\mathbf{0}$ and

$$\tilde{R}_{n+1}^T \tilde{G}(\tilde{R}^*) = R_{n+1}^{(m+1)} \tilde{G}^{(m+1)}(\tilde{R}^*),$$

we have:

RESULT 6. *Under the generic condition that*

$$\{\tilde{R}_i : x_i^* > 0\}$$

engenders the subspace $\tilde{\mathcal{S}}$ of all $(m+1)$ -dimensional vectors with the $(m+1)$ th component equal to 0, the phenotypic equilibrium manifold $\tilde{\mathcal{M}}^$ is LES at $(\tilde{x}^*, \tilde{R}^*)$ if $d\tilde{G}(\tilde{R}^*)$ is negative definite on $\tilde{\mathcal{S}}$ and $\tilde{G}^{(m+1)}(\tilde{R}^*) < 0$.*

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