RESEARCH ARTICLE

Evolutionary Invasion Analysis in Structured Populations

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Abstract

Evolutionary invasion analysis seeks to identify those phenotypes that cannot be invaded and replaced by alternative organismal strategies. This is achieved by first constructing a dynamical system that governs a rare mutant's dynamics when introduced into an ecological setting at equilibrium with a resident strategy. From this, a mutant fitness function is derived whose analysis is dependent on the complexity of the ecological milieu. Invasion analyses of age-, stage-, space-, or otherwise-structured populations typically require that a fitness function, termed the invasion fitness, be extracted as an eigenvalue of the linearized dynamics of the focal organism's ecology. This poses little technical difficulty when populations are structured into a small number (usually < 4) of compartments. However, for more complex ecologies, calculating the invasion fitness can be difficult. Here we present an algorithm to perform such analyses in class-structured populations, even when the resulting dimensionality is high enough to prohibit the direct calculation of a dominant eigenvalue. This algorithm also allows for an assessment of the evolutionary stability and convergence stability conditions, thus providing a tool for the complete evolutionary analysis of class-structured populations.

Keywords Evolutionary stability · Mutant · Game theory · Dynamics · Convergence stability

Introduction

Evolutionary invasion analysis (Dieckmann & Law, 1996; Geritz et al., 1998a; Hamilton, 1967; Metz et al., 1992, 1996) is a highly utilized framework for the development and analysis of models of phenotypic evolution, having been profitably employed in the development of a vast literature including topics such as sperm competition, evolution of dispersal, interfamilial conflicts, as well as the rich literature arising from questions of evolutionary epidemiology (see (Nowak & Sigmund, 2004) for a review). By providing the mathematical underpinnings of these discussions with an evolutionary framework broadly consistent with many real-world situations, evolutionary invasion analysis has come to be an essential tool in the evolutionary ecologists' theoretical toolbox. In the literature it is often associated with evolutionary game theory. However, where invasion analysis is a universal, first principles based, technical tool, evolutionary game theory is primarily a language for the formulation and communication of theoretical intuitions about an important subset of ecological mechanisms.

To conduct an evolutionary invasion analysis, one first starts with an ecological model of the temporal dynamics of some population of an organism of interest, as well as a model of how often mutations in the organismal trait being modeled arise, and how these mutational variants either spread to fixation, or eventually go extinct. Mutations are assumed to be rare events; mutation-generated phenotypes of potential invaders can thus be envisioned as arising in an ecological setting in which the resident type is near its ecological equilibrium. Questions of invasion of a novel type are therefore dealt with by utilizing the tools of linear stability analyses, wherein the fate of a mutant is studied via the behavior of its population growth rate, termed its invasion fitness (Metz, 2008; Metz & Geritz, 2016; Otto & Day, 2007), when it is initially introduced as a small departure from the stable equilibrium the population occupied in the mutant's absence.

In the simplest case the mutant is a single type of organism, and the evolutionary analysis consists of the optimization of an easily derived expression for the mutant population growth-rate as a function of the value of the metric trait

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of interest in both the mutant and the resident population of organisms, followed by solving the equation that results from choosing the mutant's trait value to be equal to that of the resident (so that individuals sporting the so found trait value do better than any mutants). However, in many cases a more realistic treatment of ecological dynamics requires accounting for the possibility of heterogeneity in the population dynamical effects of the trait of interest, which depends on some property of the specific organism in which the trait is being expressed (Otto & Day, 2007).

This phenomenon corresponds to some kind of structure in the organism's population, like age (here we assume that organisms can be grouped into discrete age classes), stage, or some other (discrete) measure of an organism's state. For example, a case where a group of interacting species, genotypes, or phenotypes, all share a common pathogen, whose virulence (pathogen-induced host death rate) depends on the type of host it occupies. Thus, a given level of exploitation by the pathogen will result in different expected pathogen lifespans (e.g. in healthy versus immune-compromised hosts), with the risk of ending the infection due to host death depending on the type of host it is currently infecting. Infections in each host type thus represent different infection classes and infection dynamics must be followed for each of them (Williams, 2011). While the process of analyzing these more complex ecological situations remains the same, in principle, as in the case without some sort of population structure, the actual mathematical techniques are less rigorously established in cases where focal organisms come in multiple types, so that the ecological dynamics are multi-dimensional. Indeed, as researchers explore more and more complicated ecological models that explicitly address trait heterogeneity, calculating the mutant growth rate distills down to finding the dominant eigenvalue of an $n \times n$ matrix (for n population classes). However, since this in general becomes algebraically impossible for $n \geq 4$, a straightforward 'recipe' will be of considerable help for analyzing such games (Hurford et al., 2010). In this work we provide a general algorithm for calculating the basic terms required to perform an evolutionary invasion analysis for populations structured into an arbitrary number of classes. For the main development, we treat the case wherein temporal dynamics are assumed continuous but, in the appendix (S1), we provide the toolbox for the discrete time case as well. By this approach, we present a systematic and general tool for conducting evolutionary invasion analyses in highly structured populations.

The expressions derived either below or in Metz and Leimar (2011) enable local ESS calculations for general ecological scenarios, where 'local' means that any mutant that attempts to invade does not differ too much from the resident. The underlying idea, but not the algebraic tools crafted from it, already is touched upon in (Metz & Leimar, 2011

and references therein). The present paper adds effective algebraic recipes for putting that tool to work, while (Metz & Leimar, 2011) show that under certain mild conditions (the trait space should be connected and the demographic parameters should be continuous in the trait vector) such tools can even be used to decide whether or not a local ESS result extends to a global one, allowing any amount of dissimilarity between mutant and resident, although doing so in practice usually requires considerable mathematical effort in addition to some luck.

Methods

We assume the ecological dynamics of a structured population can be described by a continuous-time (discrete-time in Appendix S1) dynamical system of the form

$$\dot{x} = F(x) \tag{1}$$

where x_i is the number (proportion, density, etc.) of organisms in a group (age-group, subpopulation, class, etc.) $x = (x_1, x_2, \cdots, x_n)$, $\dot{x}$ represents the time derivative of the population vector x, and $F : R^n \to R^n$ is a function that maps the population vector, x, to another population vector, x', according to the population update rule summarized by (the generally nonlinear) vector-valued function, $F = (F_1, F_2 \cdots, F_n)$, where the functions, $F_i : R^n \to R$, for $i = 1, \cdots, n$, determine the temporal dynamics of the x_i's by encapsulating the salient ecological features of their survival and reproduction (Reed & Stenseth, 1984).

To introduce evolution into this ecological framework, it is assumed that some model parameters, p, are determined by some heritable, quantitative, scalar trait, ε, or a vector of such traits, so that we can write $p \equiv p(\varepsilon)$. It is further assumed that mutations occur infrequently enough that a resident population is always at (or very close to) an equilibrium of the system (1). Finally, ecological dynamics are presumed to proceed much more rapidly than evolutionary ones, so that those mutations that are fitter than the resident variant are assumed to replace the formerly resident variant essentially instantaneously on an evolutionary timescale. With these considerations, (1) may be extended to allow for the study of evolutionary outcomes by writing the initial dynamics of the rare mutant variant (indicated by the '~' symbol) as the linear approximation

$$\dot{\tilde{x}} = A\tilde{x}, \tag{2}$$

where the matrix A is given by $[A]_{ij} \equiv \partial F_i / \partial x_j$, evaluated at the resident equilibrium (and the mutant extinction boundary). This introduces a dependence of A on $\hat{x}$, i.e. the equilibrium values of x, and hence on ε. Thus, $A \equiv A(\tilde{\varepsilon}, \varepsilon)$, and

the fate of the mutant is determined by the dominant eigenvalue, $\lambda_1(\tilde{\varepsilon}, \varepsilon)$, of this matrix (Otto & Day, 2007), with

$$\lambda_1 < 0 \iff \text{extinction}$$

$$\lambda_1 > 0 \iff \text{invasion.} \tag{3}$$

Provided the parameter under evolutionary control comes not too close to a community dynamical bifurcation point, in many cases, in particular for small mutational steps, invasion implies substitution (Dercole & Geritz, 2016; Dercole & Rinaldi, 2008; Geritz, 2005; Geritz et al., 2000; Priklopil & Lehmann, 2020). In order not to complicate the argument we proceed on the assumption that the latter is the case. For many models repeated iterations of this process then converge on a strategy, ε^*, that cannot be invaded by any other nearby mutants. Such an evolutionarily stable strategy (ESS) of (2) thus maximizes $\lambda_1(\tilde{\varepsilon}, \varepsilon)$ in its first argument. Analytically then, a putative ESS, ε^*, must satisfy the conditions

$$\text{(i)} \quad \left.\frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}\right|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} = 0 \text{ and (ii)} \quad \left.\frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon}^2}\right|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} < 0. \tag{4}$$

In addition, a third condition governing the evolutionary attainability of the above ESS must be met:

$$\left(\frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon}^2} + \frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon} \partial \varepsilon}\right)_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} < 0, \text{ or equivalently } \left(\frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon}^2} - \frac{\partial^2 \lambda_1}{\partial \varepsilon^2}\right)_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} < 0, \tag{5}$$

This last inequality, the CS condition, ensures local convergence towards the ESS, so that the ESS is attracting, and will ultimately be reached through this evolutionary process (Eshel, 1983). The alternative, occurring in certain situations, is that expression (4ii) fails to hold, so that the evolutionarily critical point, ε^*, identified in (4i) is not an ESS, despite being a CS, since expression (5) still holds. Such points are termed evolutionary branching points due to the fact that upon arriving there, evolution favors a paired movement away from that point, which has been interpreted as the evolution of lineage splitting [(Geritz et al., 1998b); for the case where epsilon is a vector see Sect. 5 of Metz and Geritz (2016)].

To assess these three conditions, there are several ways to proceed. When (2) is low dimensional ($n \leq 4$), the eigenvalues of A, $\lambda_1 \geq \lambda_2 \geq \cdots \geq \lambda_n$ and more in particular the dominant eigenvalue (the one with largest real part, which in this case is just real), can usually be directly calculated as functions of the mutant and resident strategies by solving for the roots of the characteristic equation, i.e., symbolically solving $C(\lambda) = 0$ (using e.g. Matlab, Maple, or Mathematica), where

$$C(\lambda) \equiv det(A - \lambda I) = a_0 \lambda^n + a_1 \lambda^{n-1} + a_2 \lambda^{n-2} + \cdots + a_{n-1} \lambda + a_n C(\lambda)$$
$$\equiv det(A - \lambda I) = a_0 \lambda^n + a_1 \lambda^{n-1} + a_2 \lambda^{n-2} + \cdots + a_{n-1} \lambda + a_n \tag{6}$$

Conditions (4i)–(5) can then be evaluated. (It should be noted though that already in the case $n = 2$ the resulting expressions are not particularly easy to handle, so even here the methods developed below may be preferred above the brute force approach.) For larger dimensional systems, explicit solutions of (6) are generally impossible. In such cases, analyses have proceeded along two additional routes (Otto & Day, 2007). First, a well-known result from linear algebra states that

$$\lambda_1(\tilde{\varepsilon}, \varepsilon) = \frac{\tilde{v}(\tilde{\varepsilon}, \varepsilon) A(\tilde{\varepsilon}, \varepsilon) \tilde{u}(\tilde{\varepsilon}, \varepsilon)}{\tilde{v}(\tilde{\varepsilon}, \varepsilon) \tilde{u}(\tilde{\varepsilon}, \varepsilon)}, \tag{7}$$

where $\tilde{v}$ and $\tilde{u}$ are the dominant left and right, respectively, eigenvectors of the matrix A corresponding to the eigenvalue λ (Caswell, 2001). Using this expression, it can be shown that

$$\left.\frac{\partial \lambda}{\partial \tilde{\varepsilon}}\right|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} = \left.\frac{v \partial A/\partial \tilde{\varepsilon} u}{v u}\right|_{\varepsilon=\tilde{\varepsilon}=\varepsilon^*}, \tag{8}$$

where v and u are the dominant left and right eigenvectors of the matrix $A(\varepsilon, \varepsilon)$ (Taylor & Frank, 1996). Despite the simplicity of the first order condition (8), some potential difficulties arise when utilizing this method. In this approach, the dominant left eigenvector of $A(\varepsilon, \varepsilon)$ needs to be calculated, which can be both difficult and time-consuming. [The dominant right eigenvector of $A(\varepsilon, \varepsilon)$ is proportional to the resident's class distribution, which has to be calculated anyway in order to calculate $A(\varepsilon, \varepsilon)$.] Moreover, the second order conditions that need to be satisfied in order for a singular strategy [that is, a solution of (4i)] to be an ESS and CS are even less easily calculated, as their evaluation requires calculating derivatives of the dominant eigenvectors (as expressions of both $\tilde{\varepsilon}$ and ε), the avoidance of which is one of the chief values of the current approach in obtaining the first order condition (8).

Alternatively, one can, in principle, calculate the required derivatives directly from the characteristic polynomial [expression (6) of $A(\tilde{\varepsilon}, \varepsilon)$], which implicitly defines the eigenvalues in terms of the coefficients of the characteristic polynomial (Otto & Day, 2007). However, neither of the only two papers known to us to come up with such a strategy (Courteau & Lessard, 2000; Metz & Leimar, 2011) derive any general explicit expressions or algorithms for calculating the required derivatives in terms of the entries of $A(\tilde{\varepsilon}, \varepsilon)$. Indeed, often either the eigenvector method or the characteristic polynomial are used to derive a first-order condition (Eq. 4i) while second-order ESS and CS conditions (Eqs. 4ii and 5, respectively) go uncalculated (Otto & Day, 2007). Yet, a straightforward algorithm does exist for the calculation of the coefficients of the characteristic polynomial (6) when it is of arbitrary degree, and these can be used to provide a general invasion analysis recipe for class-structured populations. The most intensive calculation in this algorithm involves determining the

trace of powers of the matrix $A(\tilde{\varepsilon}, \varepsilon), A^k, k = 1, \cdots, n$ which are straightforward calculations.

For the characteristic polynomial of the matrix A in (2) written in the form (6), the coefficients of $C(\lambda)$ can be obtained from the following recursive relationships (Zadeh and Desoer 1963, pp. 303–305):

$$a_0 = (-1)^n, a_1 = -a_0 T_1, a_2 = -\frac{1}{2}[a_1 T_1 + a_0 T_2],$$
$$a_3 = -\frac{1}{3}[a_2 T_1 + a_1 T_2 + a_0 T_3], \cdots, \qquad (9)$$
$$a_n = \frac{-1}{n}[a_{n-1} T_1 + a_{n-2} T_2 + \cdots + a_1 T_{n-1} + a_0 T_n]$$

where T_k is the trace of the matrix A^k, evaluated at $\tilde{\varepsilon} = \varepsilon.k = 1, \cdots, n$

Since $C(\lambda) = 0$ holds for all solutions of the characteristic polynomial of $A(\tilde{\varepsilon}, \varepsilon)$ it must, in particular, hold for the dominant eigenvalue, denoted $\lambda_1(\tilde{\varepsilon}, \varepsilon)$. We therefore wish to write the ESS/CS conditions in terms of the characteristic polynomial coefficients, a_j, and then to write these coefficients in terms of the entries of $A(\tilde{\varepsilon}, \varepsilon)$. In continuous time (see Online Appendix 1 for discrete time development), for the first-order condition (4i) we implicitly differentiate the relationship $C(\lambda_1) = 0$ in (6), where λ_1 is the dominant eigenvalue of A, to obtain

$$\frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}[na_0 \lambda_1^{n-1} + (n-1)a_1 \lambda_1^{n-2} + (n-2)a_2 \lambda_1^{n-3} + \cdots + a_{n-1}] + \frac{\partial a_0}{\partial \tilde{\varepsilon}} \lambda_1^n$$
$$+ \frac{\partial a_1}{\partial \tilde{\varepsilon}} \lambda_1^{n-1} + \frac{\partial a_2}{\partial \tilde{\varepsilon}} \lambda_1^{n-2} + \cdots + \frac{\partial a_{n-1}}{\partial \tilde{\varepsilon}} \lambda_1 + \frac{\partial a_n}{\partial \tilde{\varepsilon}} = 0$$

$$(10)$$

To determine the coefficient, a_n, we can recognize that, by definition, the characteristic polynomial of A can be factored as $C(\lambda) = \prod_{i=1}^n (\lambda - \lambda_i)$, where the λ_i are the n (not necessarily distinct) eigenvalues of A. Expanding this shows that the constant term, a_n, is $(-1)^n \prod_{i=1}^n \lambda_i = (-1)^n det A$. Therefore, substituting this for a_n in (11) and equating to zero gives the first-order condition

$$\frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} = 0 \iff \frac{\partial det A}{\partial \tilde{\varepsilon}}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} = 0. \qquad (12)$$

where $det A\, det A$ is the determinant of the matrix $A(\tilde{\varepsilon}, \varepsilon) A(\tilde{\varepsilon}, \varepsilon)$. Although essential in its derivation, the truth of (12) does not hinge on a_{n-1} being unequal to zero. In cases where $a_{n-1} = 0$ we can continuously perturb the parametrized polynomial $C(\lambda; \tilde{\varepsilon}, \varepsilon)$ a little bit, to make $a_{n-1} \neq 0$. If we can choose that perturbation such that the solutions ε^* to both the left and right hand side of (12) are continuous in its parameters, then the reach of the "if and only if" in (12) also extends to the situation where $a_{n-1} = 0$.

$det A$ can be evaluated from its specification in (2) by using the standard technique of expansion-by-minors. While this calculation is easy for low dimensional systems, it becomes quite time-consuming for higher-order systems. In the latter case, the a_n can be calculated by means of recursion (9).

Moving on to the second order conditions, implicitly differentiating (10) with respect to $\tilde{\varepsilon}$ results in

$$\frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon}^2}[na_0 \lambda_1^{n-1} + (n-1)a_1 \lambda_1^{n-2} + (n-2)a_2 \lambda_1^{n-3} + \cdots + a_{n-1}] + 2\frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}\left[n\frac{\partial a_0}{\partial \tilde{\varepsilon}} \lambda_1^{n-1} + (n-1)\frac{\partial a_1}{\partial \tilde{\varepsilon}} \lambda_1^{n-2} + (n-2)\frac{\partial a_2}{\partial \tilde{\varepsilon}} \lambda_1^{n-3} + \cdots + \frac{\partial a_{n-1}}{\partial \tilde{\varepsilon}}\right]$$
$$+ \left(\frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}\right)^2 [n(n-1)a_0 \lambda_1^{n-2} + (n-1)(n-2)a_1 \lambda_1^{n-3} + (n-2)(n-3)a_2 \lambda_1^{n-4} + \cdots + 2a_{n-2}] + \frac{\partial^2 a_0}{\partial \tilde{\varepsilon}^2} \lambda_1^n + \frac{\partial^2 a_1}{\partial \tilde{\varepsilon}^2} \lambda_1^{n-1} + \frac{\partial^2 a_2}{\partial \tilde{\varepsilon}^2} \lambda_1^{n-2} + \cdots + \frac{\partial^2 a_{n-1}}{\partial \tilde{\varepsilon}^2} \lambda_1 + \frac{\partial^2 a_n}{\partial \tilde{\varepsilon}^2} = 0. \qquad (13)$$

Since $\lambda_1(\varepsilon, \varepsilon) = 0$ for all ε (because the resident population is at equilibrium), evaluating (10) at $\tilde{\varepsilon} = \varepsilon$ and rearranging gives

$$\frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} = \frac{-\frac{\partial a_n}{\partial \tilde{\varepsilon}}}{a_{n-1}}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} \quad \frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} = \frac{-\frac{\partial a_n}{\partial \tilde{\varepsilon}}}{a_{n-1}}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} \qquad (11)$$

It should be noted that a problem arises when calculating the derivative of the eigenvalue in the characteristic polynomial at $\tilde{\varepsilon} = \varepsilon = \varepsilon^* \tilde{\varepsilon} = \varepsilon = \varepsilon^*$ when $a_{n-1} = 0$ since in Eq. (11) the denominator would be zero. Therefore, one cannot use this approach to compute the desired derivatives when $a_{n-1} = 0$. However, a little further through shows that if $\lambda_1 = 0$, $a_{n-1} = 0$ if and only if λ_1 is double root of C. As such double roots are rare in these sorts of models, this restriction is not much of an issue in practice. We shall come back to this issue below.

Thus, imposing the condition that $\lambda_1(\varepsilon, \varepsilon) = 0$, as well as the first-order condition (11) that must hold at all (interior) extrema of λ_1 gives the ESS (evolutionary stability) condition as

$$\frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon}^2}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} = -\frac{\frac{\partial^2 a_n}{\partial \tilde{\varepsilon}^2}}{a_{n-1}}\Big|_{\tilde{\varepsilon}=\varepsilon=\varepsilon^*} < 0. \qquad (14)$$

In similar fashion, differentiating (12) with respect to ε leads to

$$\frac{\partial^2 \lambda_1}{\partial \varepsilon \partial \tilde{\varepsilon}}[na_0 \lambda_1^{n-1} + (n-1)a_1 \lambda_1^{n-2} + (n-2)a_2 \lambda_1^{n-3} + \cdots + a_{n-1}]$$
$$+ \frac{\partial \lambda_1}{\partial \tilde{\varepsilon}}\left[n\frac{\partial a_0}{\partial \varepsilon} \lambda_1^{n-1} + (n-1)\frac{\partial a_1}{\partial \varepsilon} \lambda_1^{n-2} + (n-2)\frac{\partial a_2}{\partial \varepsilon} \lambda_1^{n-3} + \cdots + \frac{\partial a_{n-1}}{\partial \varepsilon}\right]$$
$$+ \frac{\partial \lambda_1}{\partial \tilde{\varepsilon}} \frac{\partial \lambda_1}{\partial \varepsilon}[n(n-1)a_0 \lambda_1^{n-2} + (n-1)(n-2)a_1 \lambda_1^{n-3} + (n-2)(n-3)a_2 \lambda_1^{n-4} + \cdots + 2a_{n-2}]$$
$$+ \frac{\partial^2 a_0}{\partial \tilde{\varepsilon} \partial \varepsilon} \lambda_1^n + \frac{\partial^2 a_1}{\partial \tilde{\varepsilon} \partial \varepsilon} \lambda_1^{n-1} + \frac{\partial^2 a_2}{\partial \tilde{\varepsilon} \partial \varepsilon} \lambda_1^{n-2} + \cdots + \frac{\partial^2 a_{n-1}}{\partial \tilde{\varepsilon} \partial \varepsilon} \lambda_1 + \frac{\partial^2 a_n}{\partial \tilde{\varepsilon} \partial \varepsilon}$$
$$+ \frac{\partial \lambda_1}{\partial \varepsilon}\left[n\frac{\partial a_0}{\partial \tilde{\varepsilon}} \lambda_1^{n-1} + (n-1)\frac{\partial a_1}{\partial \tilde{\varepsilon}} \lambda_1^{n-2} + (n-2)\frac{\partial a_2}{\partial \tilde{\varepsilon}} \lambda_1^{n-3} + \cdots + \frac{\partial a_{n-1}}{\partial \tilde{\varepsilon}}\right] = 0, \qquad (15)$$

while the first derivative (of λ_1) with respect to the resident strategy is

$$\frac{\partial \lambda_1}{\partial \varepsilon} \left[n a_0 \lambda_1^{n-1} + (n-1) a_1 \lambda_1^{n-2} + (n-2) a_2 \lambda_1^{n-3} + \cdots + a_{n-1} \right]$$
$$+ \frac{\partial a_0}{\partial \varepsilon} \lambda_1^n + \frac{\partial a_1}{\partial \varepsilon} \lambda_1^{n-1} + \frac{\partial a_2}{\partial \varepsilon} \lambda_1^{n-2} + \cdots + \frac{\partial a_{n-1}}{\partial \varepsilon} \lambda_1 + \frac{\partial a_n}{\partial \varepsilon} = 0. \quad (16)$$

So using once again, that $\lambda_1(\varepsilon, \varepsilon) = 0$, (16) implies that

$$\left. \frac{\partial \lambda_1}{\partial \varepsilon} \right|_{\tilde{\varepsilon} = \varepsilon = \varepsilon^*} = - \left. \frac{\partial a_n / \partial \varepsilon}{a_{n-1}} \right|_{\tilde{\varepsilon} = \varepsilon = \varepsilon^*}, \quad (17)$$

And, therefore, evaluating (15) at $\tilde{\varepsilon} = \varepsilon = \varepsilon^*$ gives

$$\left. \frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon} \partial \varepsilon} \right|_{\tilde{\varepsilon} = \varepsilon = \varepsilon^*} = - \frac{\frac{\partial^2 a_n}{\partial \tilde{\varepsilon} \partial \varepsilon}}{a_{n-1}} + \left. \frac{\frac{\partial a_n}{\partial \varepsilon}}{a_{n-1}} \frac{\frac{\partial a_{n-1}}{\partial \tilde{\varepsilon}}}{a_{n-1}} \right|_{\tilde{\varepsilon} = \varepsilon = \varepsilon^*}. \quad (18)$$

The CS condition therefore reads

$$\left. \frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon}^2} + \frac{\partial^2 \lambda_1}{\partial \tilde{\varepsilon} \partial \varepsilon} \right|_{\tilde{\varepsilon} = \varepsilon = \varepsilon^*} = - \left(\frac{\frac{\partial^2 a_n}{\partial \varepsilon^2} + \frac{\partial^2 a_n}{\partial \tilde{\varepsilon} \partial \varepsilon}}{a_{n-1}} \right) + \left. \frac{\frac{\partial a_n}{\partial \varepsilon}}{a_{n-1}} \frac{\frac{\partial a_{n-1}}{\partial \tilde{\varepsilon}}}{a_{n-1}} \right|_{\tilde{\varepsilon} = \varepsilon = \varepsilon^*} < 0. \quad (19)$$

Discussion

Evolutionary invasion analysis provides a rational framework within which to calculate ESS phenotypes, which represent expected evolutionary endpoints, i.e. those traits expected to be encountered under some given selective regime (Geritz et al., 1998b; Rueffler & Metz, 2013). Evolutionary invasion analysis thus furnishes the user with a predictive tool for generating hypotheses about what trait-environment combinations are likely to emerge in a population. However, such predictions are sensitive to the ecological details of the population under study; better characterization of the ecological details thus leads to better forecasting of what those expected traits should be.

Most populations exhibit some type of structure, and a framework to deal with this in a straightforward, formal way is obviously desirable. As noted here and elsewhere (Metz, 2008; Metz & Leimar, 2011), invasion analyses of highly structured populations can be confronted with an impossible task when attempting to extract a fitness function from a high-dimensional matrix via its dominant eigenvalue. Herein we have taken advantage of the fact that it is only the derivatives of the fitness function, with respect to the trait of interest in the resident and mutant strains, that are required to calculate the ESS and CS conditions.

Another recent attempt to simplify evolutionary invasion analyses has focused on deriving expressions that not only quantify the fitness proxies (i.e. where for most practical purposes a quantity is equivalent to invasion fitness but is not equal to it) of a rare mutant (Metz, 2008), but also allow for an intuitive biological interpretation (Hurford et al., 2010). This work proposes utilizing next-generation (NG) methods, which essentially allow for a useful recasting of the continuous-time dynamical system in (2) as a related discrete-time process with, often-times, a more natural interpretation in terms of the biological question at hand. Doing so involves writing the matrix A in (2) as $F - V$, where element (i,j) of F gives the rate at which new individuals appear in class j per a type i individual; the matrix V quantifies the movement of individuals between classes, as well their movement out of all classes (due to death, for example). With these definitions, one then forms the matrix product FV^{-1}, whose (i,j)th entry gives the expected number of type i individuals produced by a given j individual in its lifetime (Hurford et al., 2010). This shift in perspective from a rate of production to a per-generation view is what underlies the NG methodology. Such techniques are well-known in the epidemiological literature, where the spectral radius of FV^{-1}, i.e. $\rho(FV^{-1})$ is commonly designated the 'Basic Reproduction Number', R_0, which gives the expected number of infections produced by a given infection in a wholly susceptible population (Diekmann et al., 1990; Heesterbeek, 2002; Heesterbeek & Dietz, 1996; Lion & Metz, 2018). The utility of the NG approach lies partly in the relationship between the eigenvalues of and A and FV^{-1} and their corresponding conditions for equilibrium stability (Nowak & Sigmund, 2004): letting $s(A)$ be the spectral radius of the matrix A, *i.e.* the maximum real part of the eigenvalues of A, we have that

$$s(A) \begin{array}{l} < 0 \\ > 0 \\ = 0 \end{array} \text{ if and only if } \rho(FV^{-1}) \begin{array}{ll} < 1 & \text{(stable)} \\ > 1 & \text{(unstable)} \\ = 1 & \text{(unknown)} \end{array} \quad (20)$$

Moreover, FV^{-1} is typically an easier matrix than $A = F - V$ to work with, whose eigenvalues are often easier to calculate (Williams, 2011). In fact, as pointed out in Anderson and May (1982), when new organisms are born into a single class, to be taken as the first one, the matrix FV^{-1} has all its rows but the first one equal to zero, and its single non-zero eigenvalue may be found in position (1,1) (Anderson & May, 1982). However, for many structured populations, this matrix is typically not that simple, and the techniques presented here can be utilized to derive the required first and second order conditions. For example, for a population with 5 classes, the second order conditions in (11) require that we calculate the terms $a_4 = \frac{-1}{4!} \left[T_1^4 - 6 T_1^2 T_2 + 3 T_2^2 + 8 T_1 T_3 - 6 T_4 \right]$ and $a_5 = \frac{1}{5!} \left[T_1^5 - 10 T_1^3 T_2 + 20 T_1^2 T_3 - 20 T_2 T_3 + 15 T_1 T_2^2 - 30 T_1 T_4 + 24 T_5 \right]$, where T_k is as in (9). While potentially tedious, the calculation of all terms in both coefficients requires only matrix products

and summing along diagonals, which poses no technical difficulties.

Here we have presented a general treatment of evolutionary invasion analysis techniques when populations are structured and are thus ecologically described by high-dimensional dynamical systems. Despite the potential difficulties this entails for calculating mutant growth rates, we have demonstrated that very general expressions for determining the ESS/CS status of potential evolutionary endpoints can be derived. Moreover, these expressions, being functions of the coefficients of the characteristic polynomial, can be evaluated, for particular cases, in a straightforward manner, thus a complete and easily executed evolutionary analysis is made possible by this methodology.

Declarations

Conflict of interest None.

Informed Consent Both authors consent to the publication of this manuscript.

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