



# Journal of Biological Dynamics

ISSN: 1751-3758 (Print) 1751-3766 (Online) Journal homepage: <http://www.tandfonline.com/loi/tjbd20>

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To cite this article: Benjamin J. Ridenhour & Jerry R. Ridenhour (2018) Stability of equilibria in quantitative genetic models based on modified-gradient systems, Journal of Biological Dynamics, 12:1, 39-50, DOI: [10.1080/17513758.2017.1400598](https://doi.org/10.1080/17513758.2017.1400598)

To link to this article: <https://doi.org/10.1080/17513758.2017.1400598>



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Published online: 20 Nov 2017.



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# Stability of equilibria in quantitative genetic models based on modified-gradient systems

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## ABSTRACT

Motivated by questions in biology, we investigate the stability of equilibria of the dynamical system  $\mathbf{x}' = P(t)\nabla f(x)$  which arise as critical points of  $f$ , under the assumption that  $P(t)$  is positive semi-definite. It is shown that the condition  $\int^{\infty} \lambda_1(P(t)) dt = \infty$ , where  $\lambda_1(P(t))$  is the smallest eigenvalue of  $P(t)$ , plays a key role in guaranteeing uniform asymptotic stability and in providing information on the basis of attraction of those equilibria.

## ARTICLE HISTORY

Received 13 September 2016  
Accepted 25 October 2017

## KEYWORDS



Dynamical systems; modified-gradient system; equilibria; asymptotic stability; basin of attraction

## AMS CLASSIFICATION

92B99; 34D20; 34C75; 93D20; 93D30

## 1. Introduction

The evolution of continuous phenotypes, for example height, by means of natural selection is a central theme in evolutionary biology. The breeder's equation ( $R = h^2s$ ) was first introduced by Lush in 1937 [19] to predict the change in phenotype ( $R$ ) with respect to the heritability ( $h^2$ ) and strength of natural selection ( $s$ ). In a seminal series of papers, the breeder's equation was updated to the so-called multivariate breeder's equation by Lande [13, 14] and Lande and Arnold [16]. The (multivariate) breeder's equation is often presented in varying forms such as  $\Delta\bar{z}(t) = h^2\sigma^2\partial \ln(\bar{W})/\partial\bar{z}(t)$  [13],  $\Delta\bar{z} = \mathbf{G}\nabla \ln(\bar{W})$  [14],  $\Delta\bar{z} = \mathbf{G}\mathbf{P}^{-1}\mathbf{s}$  [16], and  $\Delta\bar{z} = \mathbf{G}\beta$  [4], as well as continuous-time counterparts (i.e.  $d\bar{z}/dt$ ; [9, 13, 15]). In these equations, several equivalences exist: the heritability ( $h^2$ ) of a trait is the ratio of the additive genetic variance ( $g^2$ ) to the phenotypic variance ( $\sigma^2$ ), thus  $h^2\sigma^2 = (g^2/\sigma^2)\sigma^2 = g^2$ ; the natural selection gradient ( $\beta$ ) is the product of the inverse of the phenotypic variance–covariance matrix ( $\mathbf{P}^{-1}$ ) and the selection differential ( $\mathbf{s}$ ) which is also equivalent to gradient of the logarithm of the average fitness function ( $\nabla \ln(\bar{W})$ ), i.e.  $\beta = \mathbf{P}^{-1}\mathbf{s} = \nabla \ln(\bar{W})$ ; finally, the diagonal elements of the additive genetic variance–covariance matrix  $\mathbf{G} = g_{i,i}^2$  and similarly the diagonal elements of phenotypic variance–covariance matrix  $\mathbf{P} = \sigma_{i,i}^2$ . All of the forms of the multivariate breeder's equation reduce to the concept that the change in mean phenotype ( $\bar{z}$ ) over time is given by the product of a genetic variance–covariance matrix ( $\mathbf{G}$ ) and the gradient of the logarithm of the average fitness function ( $\nabla \ln(\bar{W})$ ). As of December 2015, Web of Science indicates that

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the papers by Lande [13, 14] and Lande and Arnold [16] have garnered at least 791, 1442, and 2852 citations, respectively, which gives some idea of the impact these works have had on evolutionary biology and related fields.

One of the critical assumptions in much of this research is that the so-called  $\mathbf{G}$ -matrix is constant. A Web of Science search indicates at least 175 papers on the constancy and form of the  $\mathbf{G}$ -matrix with 66 of those published since January 2010 (a broader search on ‘genetic constraints’ reveals many more relevant publications). The principal concern is that the  $\mathbf{G}$ -matrix limits how traits evolve and approach their evolutionary optima [1, 3, 14]. For example, Dickerson [8] studied a special case of co-linear traits which produces a  $\mathbf{G}$ -matrix with a zero eigenvalue, thus preventing evolution along some trajectories. Furthermore, Pease and Bull [23] examined ‘ill-conditioned’  $\mathbf{G}$ -matrices where the ratio of the largest to the smallest eigenvalue is large and concluded that the speed of evolution towards an optimum is greatly reduced. Other work has suggested that the number of dimensions in the system affects stability [7]. However, formal criteria for when and how an evolutionary system will converge upon an equilibrium are lacking. While most research considers  $\mathbf{G}$  to be constant, it is widely recognized that  $\mathbf{G}$  itself is expected to evolve over time [1, 2, 16, 17]. Considering  $\mathbf{G}$  to be time-varying further muddies the waters of whether such systems approach and are stable at existing equilibria and lacks formal mathematical treatment.

Similarly, considerable interest has been paid to rugged fitness landscapes where the average fitness function has multiple peaks (optima) [5, 21, 22, 24]. Exploration of fitness landscapes, in other words movement between different optima, is a key part of Wright’s shifting balance theory [25]. Despite interest in which evolutionary optimum the population mean phenotype will evolve towards, conventional wisdom that the nearest optimum is favoured or numerical methods are relied upon. In fact, some research has shown that the nearest optimum is not always the one favoured by evolution [5]. As in the case of stability analyses, no rigorous analysis of whether or not a particular optimum will be evolved towards has been performed.

The contributions of this paper are threefold. First, we rigorously analyse the modified-gradient system used to model the evolution of continuous traits for the existence and stability of equilibria. Second, by doing so, we show that the smallest eigenvalue of the  $\mathbf{G}$ -matrix – which is allowed to vary in time – plays a key role in establishing the stability of equilibria. Finally, we determine sets which are guaranteed to be part of the basin of attraction of a given equilibrium. Taken together these contributions greatly enhance our ability to analyse and understand multivariate phenotypic evolution.

## 2. Existence and stability of equilibria

With the goal of making this paper as self-contained as possible, in this section we include some definitions, mathematical preliminaries, and proofs that are rather standard. Let  $x = (x_1, x_2, \dots, x_n)$  denote a point in  $\mathbb{R}^n$ , and let  $\mathbf{x} = [x_1 \ x_2 \ \dots \ x_n]^T$  be the corresponding  $n \times 1$  vector equivalent. (Note that we are using the variable  $x$  to represent the traditional phenotype variable  $z$  found in evolutionary biology.) We use the Euclidean norm as a measure of distance and we let  $B_\delta(\bar{x}) = \{x : |x - \bar{x}| < \delta\}$  denote the open ball of radius  $\delta$  centred at  $\bar{x}$ . By a domain in  $\mathbb{R}^n$ , we mean an open connected set. A point  $\bar{x}$  of a set  $S$  is an isolated point of that set if there exists a positive radius  $\delta$  such that  $\bar{x}$  is the only point of the set  $S$  lying inside the ball  $B_\delta(\bar{x})$ . We let  $t$  be a scalar variable representing time and use

primes to denote derivatives with respect to  $t$  (hence,  $\mathbf{x}' = \mathbf{x}'(t) = d\mathbf{x}/dt$ ). The object is to determine the stability of equilibrium solutions of the  $n$ -dimensional modified-gradient system

$$\mathbf{x}' = P(t)\nabla f(x). \tag{E}$$

Note that the continuous-time multivariate breeder's equation is of this form with  $P(t)$  being the time-dependent  $\mathbf{G}$ -matrix, and  $f$  being  $\ln \bar{W}$ . It is important to notice that the right-hand side of (E) has a dependence on  $t$  thus making the equation non-autonomous. Thus, time-translates of solutions are no longer solutions (as they are in the autonomous case), standard theorems do not apply and – importantly – the smallest eigenvalue of  $P(t)$  plays a key role in what follows. We assume throughout that the following hypothesis holds:

$H_0$ :  $D$  is a domain in  $\mathbb{R}^n$ ,  $f$  is a real-valued  $C_1$  (i.e. continuous with continuous partials) function defined on  $D$ ,  $t$  is nonnegative, the gradient of  $f$  denoted by  $\nabla f$  has components which are  $C_1$  on  $D$ , and  $P(t)$  is an  $n \times n$  matrix-valued function with  $C_1$ -entries that is defined and positive semi-definite for  $t \geq 0$ .

$H_0$  guarantees that, for any  $t_0 \geq 0$  and any  $x_0$  in  $D$ , there is a unique solution of (E) satisfying the initial condition  $x(t_0) = x_0$ . The assumption that  $P(t)$  is positive semi-definite is consistent with biological applications because the  $\mathbf{G}$ -matrix is a variance–covariance matrix, and variance–covariance matrices are always symmetric, positive semi-definite matrices.

If  $f$  has an isolated maximum value at a point  $x = \bar{x}$  of  $D$ , then we know from calculus that  $\nabla f(\bar{x}) = \mathbf{0}$  so  $\mathbf{x} = \bar{\mathbf{x}}$  is an equilibrium (i.e. constant in time) solution of (E). We investigate the stability of such equilibria. Although a translation always allows one to assume the equilibrium point is at  $\mathbf{x} = \mathbf{0}$ , we will continue to assume, because of our interest in evolutionary applications, that  $\mathbf{x} = \bar{\mathbf{x}}$  is the equilibrium solution.

We let  $\lambda_1(P(t))$  denote the smallest eigenvalue of  $P(t)$  and introduce the eigenvalue condition

$$\int_0^\infty \lambda_1(P(t)) dt = \infty. \tag{EC}$$

This condition will play an important role in what follows.

Stability of an equilibrium solution  $\bar{\mathbf{x}}$  essentially means that we can guarantee that solutions stay near  $\bar{\mathbf{x}}$  provided that they start within a prescribed distance of  $\bar{\mathbf{x}}$ , while asymptotic stability means that solutions actually approach  $\bar{\mathbf{x}}$  as  $t \rightarrow \infty$  provided that they start within a prescribed distance of  $\bar{\mathbf{x}}$ . More precisely, an equilibrium solution  $\mathbf{x} = \bar{\mathbf{x}}$  of (E) is said to be *stable* if for any  $\varepsilon > 0$ , there exists a  $\delta_\varepsilon > 0$  and a  $t_\varepsilon \geq 0$  such that any solution  $\mathbf{x} = \mathbf{x}(t)$  of (E) satisfying the initial condition  $|\mathbf{x}(t_0) - \bar{\mathbf{x}}| < \delta_\varepsilon$  for some  $t_0 \geq t_\varepsilon$  also exists and satisfies  $|\mathbf{x}(t) - \bar{\mathbf{x}}| < \varepsilon$  for all  $t \geq t_0$ . If, in addition,  $x(t) \rightarrow \bar{x}$  as  $t \rightarrow \infty$ , then the equilibrium  $\mathbf{x} = \bar{\mathbf{x}}$  is said to be *asymptotically stable*. Furthermore, *uniform stability* and *uniform asymptotic stability* occur when  $t_\varepsilon$  can be taken to be zero. Here, we are following the definitions as given on p. 40 of Hartman [11]. We note the uniformity is in the choice of starting time and differs from that of some authors (see, e.g. p. 173 of Miller and Michel [20]) where uniform asymptotic stability also involves the rate at which the different solutions tend to  $\bar{\mathbf{x}}$ .

Several other basic mathematical facts will be of use. From advanced calculus, a set in  $\mathbb{R}^n$  is compact if it is closed and bounded; furthermore, any function that is defined and

continuous on a compact set in  $\mathbb{R}^n$  assumes both a maximum and a minimum value on that set. From topology, any open set in  $\mathbb{R}^n$  consists of countably many disjoint open and connected components such that any point in the set lies in one and only one of those components. From linear algebra,  $\mathbf{x} \cdot \mathbf{y} = \mathbf{x}^T \mathbf{y}$  denotes the inner (or dot) product of vectors  $\mathbf{x}$  and  $\mathbf{y}$ . Especially important to us will be that an  $n \times n$  symmetric matrix  $S$  is positive definite (positive semi-definite, respectively) if and only if the quadratic form – defined by  $\mathbf{x}^T S \mathbf{x}$  – is positive definite (positive semi-definite, respectively); that is, if and only if  $\mathbf{x} \cdot S \mathbf{x} > 0$  ( $\mathbf{x} \cdot S \mathbf{x} \geq 0$ , respectively) for all  $\mathbf{x} \neq \mathbf{0}$ . Additionally, a symmetric matrix  $S$  has real eigenvalues and is positive definite (semi-definite, respectively) if and only if all its eigenvalues are positive (non-negative, respectively). We let  $\lambda_1(S) \leq \lambda_2(S) \leq \dots \leq \lambda_n(S)$  be the eigenvalues of a symmetric matrix  $S$  listed in increasing order. In our proof, we will focus on the smallest eigenvalue of  $P(t)$ , i.e.,  $\lambda_1(P(t))$ . In particular, we will use the fact that  $\mathbf{x} \cdot (P(t)\mathbf{x}) \geq \lambda_1(P(t))(\mathbf{x} \cdot \mathbf{x})$  for any  $\mathbf{x}$  in  $\mathbb{R}^n$ .

As a final preliminary, Lyapunov functions will play an important role in our proofs. A real-valued function  $g$  that is defined and continuous near a point  $x = \bar{x}$  in  $\mathbb{R}^n$  is said to be positive definite (positive semi-definite, respectively) at  $\bar{x}$  if  $g(\bar{x}) = 0$  and  $g(x) > 0$  ( $g(x) \geq 0$ , respectively) for all  $x \neq \bar{x}$  in some ball  $B_r(\bar{x})$  centred at  $\bar{x}$  with positive radius  $r$ . Any real-valued function  $V$  defined on the domain  $D$  may be composed with a solution  $\mathbf{x} = \mathbf{x}(t)$  of (E) to form a real-valued function  $V_{\mathbf{x}}(t) = V(\mathbf{x}(t))$  of the real variable  $t$ . If  $V$  is differentiable, then  $V_{\mathbf{x}}$  is as well; in this case, the so-called *trajectory derivative* is given by

$$\begin{aligned} V'_{\mathbf{x}}(t) &= \frac{\partial V}{\partial x_1}(\mathbf{x}(t))x'_1(t) + \frac{\partial V}{\partial x_2}(\mathbf{x}(t))x'_2(t) + \dots + \frac{\partial V}{\partial x_n}(\mathbf{x}(t))x'_n(t) \\ &= \mathbf{x}'(t) \cdot \nabla V(\mathbf{x}(t)) = -(P(t)\nabla f(\mathbf{x}(t))) \cdot \nabla f(\mathbf{x}(t)). \end{aligned}$$

If  $\mathbf{x} = \bar{\mathbf{x}}$  is an equilibrium solution of (E), then a *Lyapunov function* at  $\bar{\mathbf{x}}$  is any real-valued function  $V$  that (1) is defined and continuously differentiable on  $D$ , (2) is positive definite at  $\bar{\mathbf{x}}$ , and (3) has trajectory derivatives satisfying  $V'_{\mathbf{x}}(t) \leq 0$  for  $t \geq 0$ .

Given the preceding preliminaries, now consider the following hypotheses:

- $H_1$ :  $f$  has an isolated local maximum value at the point  $\bar{x} \in D$ ;
- $H_2$ :  $\bar{x}$  is an isolated critical point of  $f$ ; and
- $H_3$ : eigenvalue condition (EC) holds.

Note that  $H_1 \not\Rightarrow H_2$  and  $H_2 \not\Rightarrow H_1$  on  $D$ . Our stability results are contained in the following theorem.

**Theorem 2.1 (Stability and Asymptotic Stability):**

- (i) If  $H_0$  and  $H_1$  hold, then  $x = \bar{x}$  is a uniformly stable equilibrium solution of (E).
- (ii) If  $H_0, H_1, H_2$  and  $H_3$  all hold, then  $x = \bar{x}$  is a uniformly asymptotically stable equilibrium solution of (E).

**Proof:** (i) follows from standard Lyapunov theorems (see, for example, Theorem 8.3, p. 40 in Hartman [11]); however, we include a proof here in the interest of making this paper self-contained and because it leads into the proof of (ii). Suppose  $H_0$  and  $H_1$  hold. Let  $\varepsilon > 0$  be given. Let  $M = f(\bar{x})$ . Choose  $r > 0$  with  $r < \varepsilon$  and such that  $f(x) \leq M$  for  $|x - \bar{x}| < r$ . Since  $f$  has an isolated maximum value at  $\bar{x}$ , we may also assume that  $f(x) < M$  when  $0 < |x - \bar{x}| \leq r$ .

Let  $V$  be defined on  $D$  by  $V(x) = M - f(x)$ . Then  $V$  is a Lyapunov function at  $\bar{x}$  since  $V$  is positive definite at  $\bar{x}$  and the trajectory derivative

$$V'_x(t) = -\nabla f(x(t)) \cdot x'(t) = -\nabla f(x(t)) \cdot P(t)\nabla f(x(t)), \tag{TD}$$

is nonpositive since  $P(t)$  is positive semi-definite. On the closed and bounded set  $S = \{x : |x - \bar{x}| = r\}$ ,  $V$  is positive and continuous and hence has a minimum value, call it  $m$  with  $m > 0$ . Because  $V$  is continuous and  $V(\bar{x}) = 0$ , we choose  $\delta > 0$  such that  $V(x) < m$  for  $|x - \bar{x}| < \delta$ . Consider any trajectory  $x(t)$  of (E) that satisfies  $|x(t_0) - \bar{x}| < \delta$  for some  $t_0 \geq 0$ . Then  $V_x(t_0) = V(x(t_0)) < m$ . Because  $V_x$  is nonincreasing for  $t \geq t_0$ , the trajectory  $x(t)$  can never reach the set  $S$  where we would have  $V(x(t)) \geq m$ . Therefore, (see, e.g. Theorem 3.1, pp. 12–13 of Hartman [11]) we see that  $x(t)$  exists for all  $t \geq t_0$ ; hence,  $x(t)$  stays in  $B_r(\bar{x})$  and therefore in  $B_\varepsilon(\bar{x})$ . This proves (i).

Now assume  $H_0, H_1, H_2$ , and  $H_3$  all hold. Let  $M$  and  $V$  be defined as in the proof of (i). Suppose  $\varepsilon > 0$ . Because  $\bar{x}$  is an interior point of  $D$  (i.e. it is not on the boundary of  $D$ ) and since  $H_1$  and  $H_2$  hold, we can restrict  $\varepsilon$  to be so small that  $x \in D, f(x) < M$  and  $\nabla f(x) \neq \mathbf{0}$  for  $0 < |x - \bar{x}| \leq \varepsilon$ . Since we have uniform stability by Part (i), we find  $\delta > 0$  with  $\delta < \varepsilon$  such that any solution  $x(t)$  satisfying  $|x(t_0) - \bar{x}| < \delta$  at some time  $t_0 \geq 0$  also satisfies  $|x(t) - \bar{x}| < \varepsilon$  for all  $t \geq t_0$ .

Let  $x(t)$  be any solution with  $|x(t_0) - \bar{x}| < \delta$  at some time  $t_0 \geq 0$ . To complete the proof of Part (ii), we need to show that  $\lim_{t \rightarrow \infty} x(t) = \bar{x}$ . Since we have uniqueness of solutions to initial value problems, we can assume  $x(t) \neq \bar{x}$  for  $t \geq t_0$ . Also, for  $t \geq t_0$ ,  $P(t)$  is positive semi-definite and  $|x(t) - \bar{x}| < \varepsilon$  so we have  $V_x(t) = M - f(x(t)) > 0$  and  $V'_x(t) = -(P(t)\nabla f(x(t))) \cdot \nabla f(x(t)) \leq 0$ . Therefore,  $c \equiv \lim_{t \rightarrow \infty} V_x(t)$  exists with  $c \geq 0$ . We prove that  $c = 0$ . Suppose not, then  $c > 0$ . Since  $V(\bar{x}) = 0$ , we use the continuity of  $V$  to choose  $\delta_1$  with  $0 < \delta_1 < \delta$  so that  $V(x) < c$  for  $|x - \bar{x}| < \delta_1$ . Because  $V_x(t) = V(x(t)) > c$  for all  $t \geq t_0$ , the trajectory  $x(t)$  stays in the region  $\{x : \delta_1 \leq |x - \bar{x}| \leq \varepsilon\}$  for all  $t \geq t_0$ . On this compact region, the continuous function  $\nabla f(x) \cdot \nabla f(x)$  is positive and hence assumes a positive minimum value  $m_1$  at some point in the set. Hence, for  $t \geq t_0$ , we get that

$$V'_x(t) \leq -\lambda_1(P(t))\nabla f(x(t)) \cdot \nabla f(x(t)) \leq -m_1\lambda_1(P(t)).$$

Consequently,

$$V_x(t) = V_x(t_0) + \int_{t_0}^t V'_x(s) \, ds \leq V_x(t_0) - \int_{t_0}^t m_1\lambda_1(P(s)) \, ds,$$

for  $t \geq t_0$ . But then (EC) implies that  $V_x(t) \rightarrow -\infty$  as  $t \rightarrow \infty$  contradicting that  $V_x(t)$  stays positive. This proves that  $\lim_{t \rightarrow \infty} V_x(t) = 0$ .

Finally, we prove that  $\lim_{t \rightarrow \infty} x(t) = \bar{x}$ . Suppose not. Then there exists  $\varepsilon_1$  with  $0 < \varepsilon_1 < \varepsilon$  and arbitrarily large values of  $t$  where  $|x(t) - \bar{x}| \geq \varepsilon_1$ . For such  $t$ ,  $V_x(t) = V(x(t)) \geq m_2$  where  $m_2$  is defined to be the minimum value of  $V(x)$  on the compact set  $\{x : \varepsilon_1 \leq |x - \bar{x}| \leq \varepsilon\}$ . Because  $m_2 > 0$ , this contradicts  $\lim_{t \rightarrow \infty} V_x(t) = 0$  completing the proof. ■

**Example 2.1:** *Asymptotic Stability requires Eigenvalue Condition.* The following example illustrates that an eigenvalue condition, such as we have given in (EC), is necessary in order to obtain asymptotic stability; that is, if the eigenvalues are too small, then asymptotic stability may not occur.

Let  $P(t) = \begin{bmatrix} (t+1)^{-2} & 0 \\ 0 & (t+1)^{-1} \end{bmatrix}$  and  $f(x_1, x_2) = 4 - (x_1 - 1)^2 - (x_2 - 1)^2$  and consider the system

$$\mathbf{x}' = \begin{bmatrix} x_1' \\ x_2' \end{bmatrix} = P(t)\nabla f(\mathbf{x}) = \begin{bmatrix} -2(x_1 - 1)(t + 1)^{-2} \\ -2(x_2 - 1)(t + 1)^{-1} \end{bmatrix}, \quad \text{for } t \geq 0.$$

Then  $\lambda_1(P(t)) = (t + 1)^{-2}$  and  $\lambda_2(P(t)) = (t + 1)^{-1}$  so  $\int_0^\infty \lambda_1(P(t)) dt < \infty$  while  $\int_0^\infty \lambda_2(P(t)) dt = \infty$ . Hence, Theorem 2.1(i) applies to show that the equilibrium solution  $x_1(t) \equiv 1$ ,  $x_2(t) \equiv 1$  where the maximum value of  $f$  occurs is a uniformly stable equilibrium solution, but Theorem 2.1(ii) does not apply to give that the equilibrium solution is asymptotically stable. In fact, the system is uncoupled and is easy to solve in closed form to get that the general solution is given by  $x_1(t) = 1 + c_1 \exp(2/(t + 1))$ ,  $x_2(t) = 1 + c_2(t + 1)^{-2}$  where constants  $c_1$  and  $c_2$  depend upon the initial conditions. We see that the  $x_1$ -component of a solution starting at a point where  $x_1 \neq 1$  does not tend to 1 as  $t \rightarrow \infty$ , rather it approaches  $1 + c_1$ ; hence the equilibrium solution is not asymptotically stable. Of course, we do obtain  $\lim_{t \rightarrow \infty} x_2(t) = 1$  since the one-dimensional differential equation for  $x_2$  involves only the eigenvalue  $\lambda_2(P(t))$  and  $\int_0^\infty \lambda_2(P(t)) dt = \infty$ .

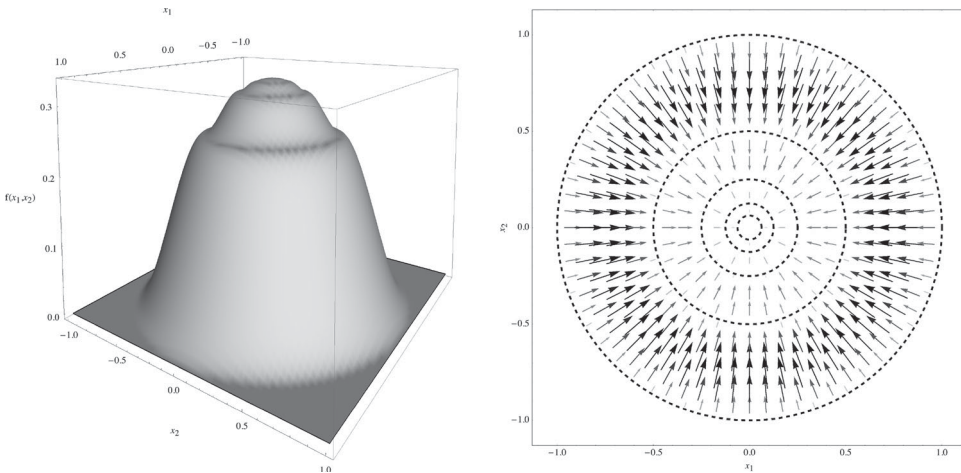
Next, we produce an example which shows that the hypothesis  $H_2$  is essential to the conclusion that  $\mathbf{x} = \bar{\mathbf{x}}$  is asymptotically stable when  $P(t)$  satisfies (EC) as in Theorem 2.1(ii). More specifically, if  $f$  has an isolated local maximum at  $\bar{\mathbf{x}}$  but  $\bar{\mathbf{x}}$  is not an isolated critical point, then we can only conclude stability, not asymptotic stability. Even for gradient systems (that is, the case where  $P(t)$  is the constant identity matrix), the necessity of adding the assumption that the point where the isolated local extremum occurs is also an isolated critical point seems to have been missed by some authors – see Part 3 of the theorem on page 205 of Hirsch *et al.* [12] as an example.

**Example 2.2:** *Asymptotic Stability requires Isolated Critical Point.* The goal is to produce a radially symmetric function  $f(r, \theta)$  using polar coordinates that is continuously differentiable on the unit circle  $r \leq 1$ , that has an absolute maximum value at the origin, that decreases as  $r$  increases, and is such that there is a sequence of concentric circles  $r = r_i$  with  $r_i$  decreasing to zero as  $i \rightarrow \infty$  and with each  $r = r_i$  consisting entirely of critical points of  $f$ . We again let  $P(t)$  be the  $2 \times 2$  identity matrix, thus satisfying (EC). The system  $\mathbf{x}' = P(t)\nabla f$  will then have the properties we seek, namely, we no longer have isolated critical points of  $f$ .

We first define sequences  $x_n$  and  $z_n$  by  $x_n = -2^{-n}$  and  $z_n = (1 - 4^{-n})/3$  for  $n = 0, 1, 2, \dots$ . Let  $I_n$  be the interval  $[x_n, x_{n+1}]$ . The union of the intervals  $I_n$  is then the interval  $[-1, 0)$ . We define a function  $p(x)$  on the interval  $[-1, 0)$  which is restricted to the interval  $I_n$  is a cubic polynomial  $p_n(x)$ . Furthermore, we require each  $p_n(x)$  to satisfy

$$p_n(x_n) = z_n, \quad p_n'(x_n) = 0, \quad p_n(x_{n+1}) = z_{n+1}, \quad p_n'(x_{n+1}) = 0. \tag{1}$$

Letting  $p_n(x) = \alpha(x - x_n)^3 + \beta(x - x_n)^2 + \gamma(x - x_n) + \delta$  and using the requirements in (1), we find after some algebra and calculus that  $\alpha = -2^{n+2}$ ,  $\beta = 3$ ,  $\gamma = 0$  and  $\delta = (1 - 4^{-n})/3$ . We then find, again using calculus, that  $p_n'(x) > 0$  for  $x$  in the open interval  $(x_n, x_{n+1})$  and the maximum value of  $p_n'$  on the interval  $I_n$  is  $3/2^{n+2}$ . We then extend  $p(x)$



**Figure 1.** Graph of the bivariate polynomial spline used in Example 2.2 and the associated phase portrait. The dotted lines in the phase portrait indicate the locations the critical points given by concentric circles of radius  $r_i = 2^{-n}$  (only  $n = 0, 1, 2, 3, 4$  are shown). The vector field clearly shows asymptotic stability will not occur because a trajectory starting outside  $r = r_i$  is ‘trapped’ away from  $\bar{x}$  by the circle  $r = r_i$  and cannot approach  $\bar{x}$  as  $t \rightarrow \infty$ . The smaller vectors indicate the diminished magnitude of change in the vicinity of critical points.

to the closed interval  $[-1, 0]$  by defining  $p(0) = 1/3$ . This makes  $p$  continuous on  $[-1, 0]$ . Considering difference quotients, it is easy to see that the left-hand derivative of  $p$  at  $x = 0$  exists and has value zero. We symmetrically extend the definition of  $p$  to the interval  $[-1, 1]$  by letting  $p(x) = p(-x)$  for  $0 < x \leq 1$ . Taking into account the way the cubic polynomials were pieced together at the endpoints and the fact that the maximum value of  $p'(x)$  on the interval  $I_n$  approaches zero as  $n \rightarrow \infty$ , we see that  $p$  has a continuous derivative on the interval  $[-1, 1]$ .

Finally, we define the radially symmetric  $f(r, \theta) = f(r)$  by taking  $f(r) = p(r)$  for  $0 \leq r \leq 1$ ,  $0 \leq \theta \leq 2\pi$ . Clearly, at any point on a circle  $r = |x_n|$ , we have  $f_r = f_\theta = 0$  since  $p'(x_n) = 0$  and  $f$  is independent of  $\theta$ . Hence, all points on  $r = |x_n|$  are critical points of  $f$  and yield equilibrium solutions of  $\mathbf{x}' = \nabla f$ . Even though  $f$  has an isolated maximum value at the origin,  $x = (0, 0)$  is not an asymptotically stable equilibrium solution since solutions starting at  $t = 0$  between two concentric circles  $r = |x_n|$  and  $r = |x_{n+1}|$  are trapped in that region and cannot approach the origin as  $t \rightarrow \infty$ . Of course, Theorem 2.1(i) still applies to give that  $x = (0, 0)$  is a stable equilibrium. Figure 1 shows the graph of the radially symmetric cubic spline  $f$  and the associated phase portrait for this system.

Some general remarks can be made regarding when (EC) might be satisfied. From a mathematical perspective, as long as  $\lambda_1(P(t))$  decreases at a slow enough rate, then the integral will diverge to infinity. Thus, for example, if  $\lambda_1(P(t))$  is decreasing at a rate proportional to  $1/t$ , then (EC) will be met. However, if  $\lambda_1(P(t))$  is decreasing at a much faster rate proportional to  $1/t^2$ , then the integral will converge and (EC) is not satisfied. From a biological perspective, little is known about how  $P(t)$  evolves. Typically,  $P(t)$  is assumed to be constant, though this has been a subject of debate. As long as a zero eigenvalue does not exist, (EC) will be satisfied under the assumption of constancy. Zero eigenvalues are rarely (if ever) found in empirical studies of  $P(t)$ .



### 3. Basin of attraction

Given a uniformly asymptotically stable equilibrium  $\bar{x}$  of (E), it is of interest to know the set of points  $x_0$  such that the trajectory starting at point  $x_0$  at some time  $t_0$  exists for all  $t \geq t_0$  and approaches  $\bar{x}$  as  $t$  tends to infinity; that is, the so-called *basin of attraction* of  $\bar{x}$ . The following theorem provides information on the basin of attraction in the setting of Theorem 2.1(ii).

**Theorem 3.1 (Basin of Attraction):** *Suppose  $H_0, H_1, H_2,$  and  $H_3$  all hold. Let  $M = f(\bar{x})$ , let  $c$  be a real number less than  $M$  and let  $O_{c,\bar{x}}$  be the set defined by  $O_{c,\bar{x}} = \{\bar{x}\} \cup \{x : c < f(x) < M\}$ . Then  $O_{c,\bar{x}}$  is open and has a unique component  $E_{c,\bar{x}}$  that contains  $\bar{x}$ . Let  $\partial E_{c,\bar{x}}$  denote the boundary of  $E_{c,\bar{x}}$ , and let  $\overline{E_{c,\bar{x}}} = E_{c,\bar{x}} \cup \partial E_{c,\bar{x}}$  denote the closure of  $E_{c,\bar{x}}$ . Consider additional hypotheses:*

$H_4 : E_{c,\bar{x}}$  is bounded and  $\overline{E_{c,\bar{x}}}$  is contained in  $D$ ;

$H_5 : f(x) = c$  for all  $x$  in  $\partial E_{c,\bar{x}}$ ; and

$H_6 : f$  has no critical points other than  $\bar{x}$  in  $\overline{E_{c,\bar{x}}}$ .

If  $H_4, H_5,$  and  $H_6$  also hold, then  $E_{c,\bar{x}}$  is contained in the basin of attraction of  $\bar{x}$ .

**Proof:** Suppose  $H_0$  through  $H_6$  all hold. Let  $M, c$  and  $O_{c,\bar{x}}$  be as defined above. We first prove  $O_{c,\bar{x}}$  is open. By the continuity of  $f$ , the set  $\{x : c < f(x) < M\}$  is open. Using the continuity of  $f$  and the fact that  $f$  has an isolated maximum value at  $\bar{x}$ , choose  $\delta > 0$  such that  $f$  is defined on the ball  $B_\delta(\bar{x})$ ,  $f(x) < M$  for  $0 < |x - \bar{x}| < \delta$  and  $|f(x) - M| < M - c$  for  $x \in B_\delta(\bar{x})$ . Then  $c < f(x) < M$  for  $0 < |x - \bar{x}| < \delta$  so  $B_\delta(\bar{x})$  is open, contains  $\bar{x}$ , and is contained in  $O_{c,\bar{x}}$ . It follows that the set  $O_{c,\bar{x}} = B_\delta(\bar{x}) \cup \{x : c < f(x) < M\}$  is open. Hence, there is a unique open component  $E_{c,\bar{x}}$  of  $O_{c,\bar{x}}$  that contains the point  $\bar{x}$ .

Let  $x_0$  be any point of  $E_{c,\bar{x}}$  and let  $x(t)$  be the solution of (E) satisfying the initial condition  $x(t_0) = x_0$  for some  $t_0 \geq 0$ . We wish to prove that  $x(t)$  exists for  $t \geq t_0$  and  $\lim_{t \rightarrow \infty} x(t) = \bar{x}$ . This is clearly true if  $x_0 = \bar{x}$  so we assume  $x_0 \neq \bar{x}$  and, in light of the uniqueness of solutions to initial value problems, that  $x(t) \neq \bar{x}$  for all  $t \geq t_0$ . As before, we let  $V(x) = M - f(x)$  for  $x$  in  $D$ . While the trajectory  $x(t)$  remains in  $E_{c,\bar{x}}$ , we have by  $H_6$  that the trajectory derivative satisfies  $V'_x(t) = -P(t)\nabla f(x(t)) \cdot \nabla f(x(t)) < 0$ . Because  $V_x(t_0) < M - c$  and  $V_x(t)$  decreases as  $t$  increases, the trajectory  $x(t)$  can never reach  $\partial E_{c,\bar{x}}$  where, by  $H_5$ ,  $V_x(t)$  would equal  $M - c$ . Hence,  $x(t)$  stays in the region  $E_{c,\bar{x}}$  and therefore in the set  $\overline{E_{c,\bar{x}}}$  so long as the solution  $x(t)$  continues to exist. By  $H_4$ ,  $\overline{E_{c,\bar{x}}}$  is both closed and bounded and therefore compact. Since  $x(t)$  stays in a compact subset of  $D$ , it follows directly from Theorem 3.1 of Hartman [11], that the right-maximal interval of existence of  $x(t)$  as a solution of (E) cannot be of the form  $[t_0, \omega)$  with  $\omega < \infty$ . Thus, the solution  $x(t)$  exists for all  $t \geq t_0$ .

From here on, the proof essentially follows that of Theorem 2.1(ii), but we repeat some of the details for clarity. First, let  $\lim_{t \rightarrow \infty} V_x(t) = \alpha$  and suppose  $\alpha > 0$ . Then using the continuity of  $V$ , find  $\delta > 0$  small enough that  $0 < V(x) < \alpha$  for  $0 < |x - \bar{x}| < \delta$ . Now the set  $\overline{E_{c,\bar{x}}} \setminus B_\delta(\bar{x})$  is closed and bounded by  $H_4$ , so, by  $H_6$ , the continuous function  $\nabla f(x) \cdot \nabla f(x)$  assumes a positive minimum  $m_1$  on that set. Because  $x(t)$  never enters the set  $B_\delta(\bar{x})$  where we would have  $V_x(t) = V(x(t)) < \alpha$ , we get that  $V'_x(t) \leq -m_1\lambda_1(P(t))$  for  $t \geq t_0$ . This leads to  $V_x(t) \rightarrow -\infty$  as  $t \rightarrow \infty$ , a contradiction which shows that  $\alpha = 0$ .

The next step is to prove that  $\lim_{t \rightarrow \infty} x(t) = \bar{x}$ . To do this, suppose  $\lim_{t \rightarrow \infty} x(t) \neq \bar{x}$ . There then exists an  $\varepsilon > 0$  such that  $|x(t) - \bar{x}| \geq \varepsilon$  for arbitrarily large values of  $t$ . The function  $V(x)$  is positive and continuous on the compact set  $\overline{E_{c,\bar{x}}} \setminus B_\varepsilon(\bar{x})$ , hence,  $V(x)$  has a positive minimum, call it  $m_2$ , on the set  $\overline{E_{c,\bar{x}}} \setminus B_\varepsilon(\bar{x})$ . However, there are arbitrarily large values of  $t$  where  $x(t) \in \overline{E_{c,\bar{x}}} \setminus B_\varepsilon(\bar{x})$  for which  $V_x(t) = V(x(t)) \geq m_2$ . This contradicts  $\lim_{t \rightarrow \infty} V_x(t) = 0$  and completes the proof. ■

We note that LaSalle’s Theorem can be used to obtain information on the basin of attraction of an equilibrium solution – for example see Theorem 6.1 in Leighton [18], Theorem 11.11 in Miller and Michel [20], or the theorem on p. 200 of Hirsch *et al.* [12]. However, those results deal with autonomous systems and do not apply to (E).

We conclude by giving an example illustrating both the use of Theorem 3.1 and the role played by hypotheses  $H_5$  and  $H_6$  of that theorem.

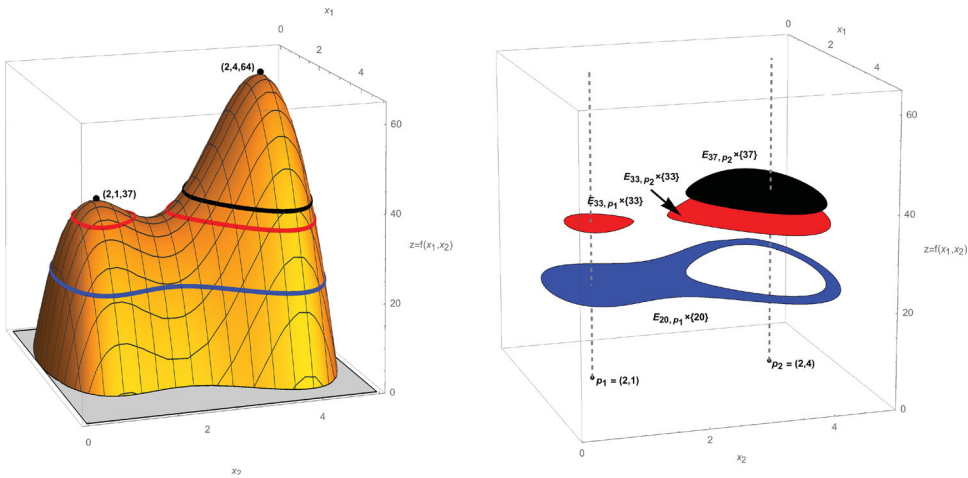
**Example 3.1:** *Basins of Attraction.* Let  $f(x_1, x_2) = 96x_2 - 84x_2^2 + 28x_2^3 - 3x_2^4 - 10(x_1 - 2)^2$ . Let  $P(t)$  be any  $2 \times 2$  matrix-valued function defined and continuous for  $t \geq 0$  and such that the eigenvalue condition (EC) holds. Equation (E) becomes

$$\begin{bmatrix} x'_1 \\ x'_2 \end{bmatrix} = P(t) \begin{bmatrix} -20(x_1 - 2) \\ -12(x_2 - 1)(x_2 - 2)(x_2 - 4) \end{bmatrix}.$$

Then  $f$  has local maximum values at the points  $p_1 = (2, 1)$  and  $p_2 = (2, 4)$  and a saddle at  $p_3 = (2, 2)$  with  $f(2, 1) = 37$ ,  $f(2, 4) = 64$  and  $f(2, 2) = 32$ . A sketch of the graph of  $f$  is shown in Figure 2.

For a real number  $c$ , let  $L_c$  denote the level set defined by  $L_c = \{(x_1, x_2) : f(x_1, x_2) = c\}$ . The level set  $L_{33}$  is shown in Figure 2.  $L_{33}$  consists of two simple closed curves; we let  $C_{p_1}$  and  $C_{p_2}$  denote the curve having the point  $p_1$  and  $p_2$  (respectively) as an interior point. Then the set  $E_{33,p_1}$  consists of all points interior to  $C_{p_1}$  while  $E_{33,p_2}$  consists of all points interior to  $C_{p_2}$ . Theorem 3.1 applies and shows that all trajectories  $x(t)$  having  $x(t_0)$  in  $E_{33,p_1}$  tend to  $p_1$  as  $t \rightarrow \infty$ , with a similar conclusion for trajectories in  $E_{33,p_2}$ . It is interesting to consider  $E_{20,p_1} = \{p_1\} \cup \{x : 20 < f(x) < 37\}$  and  $E_{20,p_2} = \{p_2\} \cup \{x : 20 < f(x) < 64\}$ . First,  $E_{20,p_2}$  contains all points interior to a simple closed curve containing both  $p_1$  and  $p_2$  in its interior; hence, Theorem 3.1 does not apply to  $E_{20,p_2}$  because  $H_6$  is violated. On the other hand,  $E_{20,p_1}$  consists of  $E_{20,p_2} \setminus \overline{E_{37,p_2}}$ . Now, Theorem 3.1 does not apply to  $E_{20,p_1}$  because the boundary of  $E_{20,p_1}$  contains points of the level set  $L_{37}$  at which  $f$  takes on the value 37 thus violating  $H_5$ ; clearly some trajectories starting in  $E_{20,p_1}$  will tend towards the boundary points in  $L_{37}$  while others will tend toward  $p_1$ .

In practice, Theorem 3.1 highlights an easy approach for biologists to understand the long-term evolutionary dynamics in their system of interest. All that needs to be established is the fitness function, such as the one plotted in Figure 2. Once the fitness function has been estimated, level sets can be drawn (by choosing various values of  $c$  to define  $E_{c,\bar{x}}$ ) to establish basins of attraction for the maxima of the function by applying the theorem. This approach might be particularly useful in the case of rugged fitness landscapes. The previous statements assume the researchers either know about  $P(t)$  or are willing to make the (commonly applied) simplifying assumptions that  $P(t)$  is constant and  $\lambda_1(P(t)) > 0$ , thus satisfying (EC).



**Figure 2.** Plot of  $f(x_1, x_2)$  from Example 3.1. In the plot on the left, the level sets  $L_{37}$  (black),  $L_{33}$  (red), and  $L_{20}$  (blue) are superimposed on the surface. A level set in  $\mathbb{R}^2$  is a curve where  $f(x_1, x_2) = c$ , thus, for example,  $L_{37}$  is the curve given by  $f(x_1, x_2) = 37$ . The plot on the right depicts the sets of points interior to the level set curves using the same colour scheme (e.g.  $E_{20, p_1}$  is blue like  $L_{20}$ ). For illustration purposes, the elevation of the set was chosen to be the number  $c$  in the definition of  $E_{c, p_i}$ ; thus the labels for each set include the cross-product with the elevation (e.g.  $E_{20, p_1} \times \{20\}$ ). Theorem 3.1 does not apply to  $E_{20, p_1}$  because the function  $f$  assumes the value 37 on the inside boundary and the value 20 on the outside boundary, thus violating hypothesis  $H_5$ .

### Conclusions

We have demonstrated conditions for the existence and stability of equilibria in modified-gradient systems. Such systems include the continuous-time multivariate breeders equation with a time-dependent  $\mathbf{G}$ -matrix which is frequently used by evolutionary biologists. Our research shows that biologists can simply search for the isolated local maxima of a fitness function; these points are guaranteed to be at least uniformly stable. Furthermore, in cases where the smallest eigenvalue of the  $\mathbf{G}$ -matrix,  $\lambda_1(P(t))$  in our notation, meets the condition  $\int_0^\infty \lambda_1(P(t)) dt = \infty$ , then the equilibrium is guaranteed to be uniformly asymptotically stable. In general this condition may be broadly met in biological systems (though this needs further testing), because the smallest eigenvalue can be decaying over time at a rate as rapid as  $1/t$  and still meet the condition. Finally, an understanding of the inverse image under the fitness function  $f$  of intervals of the form  $(c, f(\bar{x}))$  gives information on the basin of attraction of an equilibrium at  $\bar{x}$ . Thus, if biologists can easily determine  $f$ , our work shows the long-term dynamics of the traits being studied can be understood.

One of the more notable findings of this work is that, as long as (EC) is satisfied, evolution of the  $\mathbf{G}$ -matrix does not affect the stability or existence of equilibria. For the most part, biological research involving the multivariate breeder’s equation assumes that this matrix is constant in time, however this constancy has greatly been debated. Regardless of whether the  $\mathbf{G}$ -matrix remains constant, there are two main reasons to believe that (EC) will be satisfied. First, all empirical studies of the  $\mathbf{G}$ -matrix to date have found that additive genetic variation exists for all *continuous* traits under study (i.e. only those traits controlled by one or a few genetic loci— such as eye colour – are examples of traits that go to ‘fixation’).

This finding implies that there are never zero-valued eigenvalues for the  $\mathbf{G}$ -matrix. Second, mutations are known to occur regularly in the genes controlling most (if not all) phenotypes. The values of genetic variation in any trait largely end up being a balance of the force of natural selection on a trait and the mutation rate [6]. Thus the process of mutation strongly implies that some variation will exist in nearly all continuous phenotypic traits, and – even if the net genetic variation is being eroded – it is unlikely to be decaying quickly enough to violate (EC).

Our theorems imply that, if field biologists are only interested in the long-term dynamics of a system, emphasis should be placed on collecting data regarding fitness and phenotypes in order to estimate the shape of natural selection in the system. Once such data are available, it would in theory be possible to find the potential critical points of the fitness function and, accordingly, obtain information on the basins of attraction for any of the potential equilibria. This also has important implications for the shifting balance theory of evolution hypothesized by Wright [25]. One of the key phases of the shifting balance theory is that populations ‘explore’ the adaptive landscape (via processes like mutation, gene flow, or genetic drift). Some populations will pass through adaptive valleys to find new adaptive peaks (local fitness maxima) and potentially find a global fitness maximum. Theorem 3.1 details when a population will be in the basin of attraction for a potential adaptive peak. These findings also support the general concept that evolution by natural selection is a hill-climbing process and that the  $\mathbf{G}$ -matrix will rarely, if ever, prevent a system from reaching a fitness maximum in the long term.

While our work suggests that collection of data regarding the additive genetic covariance for the  $\mathbf{G}$ -matrix may be unnecessary for understanding the long-term dynamics of evolutionary systems, short-term dynamics will still be influenced by the structure of this matrix. For example, if genetic variation is lacking but not absent, then trajectories towards the nearest local maximum will proceed more slowly. Conversely, with increased genetic variation we expect the rate of evolution toward an adaptive peak to be relatively faster. This is essentially a recapitulation of the fundamental theorem of natural selection [10]. Thus depending on the application and interest (i.e. short-term versus long-term dynamics), genetic data may still be necessary to collect.

Finally, our results imply that use of adaptive dynamics may be more closely related and more similar to quantitative genetic analyses than commonly thought. Adaptive dynamic models essentially ignore genetic details of biological systems in favour of greater ecological detail. Typically, in such analyses a so-called ‘invasion fitness’ is often assumed to show when certain phenotypes may ‘invade’ a population (or other species, etc.). Traditionally the critical points and derivative of the invasion fitness are then studied to draw conclusions about ecological or evolutionary outcomes. To a certain degree, the methods of adaptive dynamics therefore parallel Theorem 2.1 and our suggested analyses of systems that involve the use of the (more) genetically explicit multivariate breeder’s equation.

## Disclosure statement

The authors have no conflicts of interest to disclose related to this research.

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