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Mutual invadability near evolutionarily singular strategies for multivariate traits, with special reference to the strongly convergence stable case

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Abstract Over the last two decades evolutionary branching has emerged as a possible mathematical paradigm for explaining the origination of phenotypic diversity. Although branching is well understood for one-dimensional trait spaces, a similarly detailed understanding for higher dimensional trait spaces is sadly lacking. This note aims at getting a research program of the ground leading to such an understanding. In particular, we show that, as long as the evolutionary trajectory stays within the reign of the local quadratic approximation of the fitness function, any initial small scale polymorphism around an attracting invadable evolutionarily singular strategy (ess) will evolve towards a dimorphism. That is, provided the trajectory does not pass the boundary of the domain of dimorphic coexistence and falls back to monomorphism (after which it moves again towards the singular strategy and from there on to a small scale polymorphism, etc.). To reach these results we analyze in some detail the

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behavior of the solutions of the coupled Lande-equations purportedly satisfied by the phenotypic clusters of a quasi-n-morphism, and give a precise characterisation of the local geometry of the set $\mathcal{D}$ in trait space squared harbouring protected dimorphisms. Intriguingly, in higher dimensional trait spaces an attracting invadable ess needs not connect to $\mathcal{D}$. However, for the practically important subset of strongly attracting esses (i.e., ess-es that robustly locally attract the monomorphic evolutionary dynamics for all possible non-degenerate mutational or genetic covariance matrices) invadability implies that the ess does connect to $\mathcal{D}$, just as in 1-dimensional trait spaces. Another matter is that in principle there exists the possibility that the dimorphic evolutionary trajectory reverts to monomorphism still within the reign of the local quadratic approximation for the invasion fitnesses. Such locally unsustainable branching cannot occur in 1- and 2-dimensional trait spaces, but can do so in higher dimensional ones. For the latter trait spaces we give a condition excluding locally unsustainable branching which is far stricter than the one of strong convergence, yet holds good for a relevant collection of published models. It remains an open problem whether locally unsustainable branching can occur around general strongly attracting invadable ess-es.

Keywords   Adaptive dynamics · Evolutionary branching · Multi-dimensional trait space · Mutual invadability · Strong attractivity · Local dimorphic divergence

Mathematics Subject Classification   92D15 · 92D25

1 Introduction

Over the last two decades *evolutionary branching* has emerged as an important concept for explaining the adaptive evolution of phenotypic diversity. Evolutionary branching occurs at points in trait space (strategies) that initially attract the evolutionary dynamics, but where selection changes from directional to disruptive once the population mean trait value comes sufficiently close (Metz et al. 1996; Geritz et al. 1997, 1998; Rueffler et al. 2006; Dercole and Rinaldi 2008; Doebeli 2011). (In line with tradition, this initial evolutionary dynamics is assumed here to be (quasi-)monomorphic. We shall below stick to this assumption, and refer to the attractors of this dynamics just as evolutionary attractors, even though branching is coincident with their repulsion in the dimorphic realm.) As a result, at such points populations can split into two or more phenotypic clusters. More specifically, evolutionary branching at a point x^* in trait space requires that at least five requirements are fulfilled (Metz et al. 1996; Geritz et al. 1998; Doebeli 2011): (i) the point x^* has to be an attractor of the evolutionary dynamics. (ii) The point x^* has to be locally invadable by mutants in at least one pair of opposite directions. (iii) In at least some of these directions nearby mutant phenotypes must be able to coexist in a protected dimorphism. (iv) There should be at least one such direction in which coexisting types experience divergent selection. (v) The coexistence cone emanating from (x^*, x^*) should be sufficiently wide for the incipient branches to stay inside while they become visibly separated. In the clonal case branching is bound to occur if these conditions are fulfilled, while in the Mendelian case these conditions are necessary, but it depends on a lot more whether branching

indeed occurs. In one-dimensional trait spaces conditions (i) to (v) are easy to check and it turns out that the former two imply the latter three (Metz et al. 1996; Geritz et al. 1997, 1998). However, in higher dimensional trait spaces this needs not to be the case. In particular, it is possible that requirement (i) and (ii) are fulfilled while (iii) is not (e.g. Doebeli 2011, p. 119), let alone (v).

In this paper we derive criteria for testing for (iii) and (v) within the reign of the local quadratic approximation for the invasion fitness function. It is known that in an n-dimensional trait space at most n + 1 branches can coexist (Durinx et al. 2008). Hence, for scalar traits, branching can only be into two. Here we show that in higher dimensional trait spaces generically any polymorphism evolves in the direction of a dimorphism (or rather, quasi-dimorphism, as close to evolutionary attractors full mutation limitation fails, so that h-morphisms get replaced by h concentrated clouds of trait values). We can therefore confine ourselves to delimiting the set $\mathcal{D}$ of trait pairs able to coexist. As final step we derive conditions for further evolution to keep a dimorphism in $\mathcal{D}$. The alternative is that the branching evolutionary trajectory falls back to monomorphism, after which it may branch again, and so on.

A next question is whether there exist restricted model classes that can be delimited in an intuitively natural manner and for which (iii) and/or (v) are implied by (i) and (ii) like in the 1-dimensional case. To discuss this question it is necessary to go a bit more deeply into the notion of attractor of the evolutionary dynamics. In one-dimensional trait spaces, whether or not a point in trait space is an attractor of the evolutionary dynamics is independent of the mutational process. In trait spaces with more than one dimension, however, the mutational input can affect the course of the evolutionary dynamics to the extent that a particular point can be an attractor for one mutational variance–covariance matrix but a repellor for another one. Leimar (2009) introduced the following notions. First, a point $\boldsymbol{x}^*$ is *absolutely convergence stable* when it is an attractor of the evolutionary dynamics for any mutational process. Second, a point $\boldsymbol{x}^*$ is called *strongly convergence stable* when it is an attractor of the evolutionary dynamics for any mutational process provided the mutational step sizes are sufficiently small. Convergence stability in this case means that $\boldsymbol{x}^*$ is an asymptotically stable fixed point of the so-called *canonical equation of adaptive dynamics* (Dieckmann and Law 1996; Champagnat 2003; Durinx et al. 2008; Champagnat and Méléard 2011; Collet et al. 2013; Metz and de Kovel 2013). Leimar (2009) furthermore established that for $\boldsymbol{x}^*$ to be robustly strongly convergence stable (below also referred to as *strongly attracting*) it is necessary and sufficient that the Jacobian matrix J of the selection gradient at $\boldsymbol{x}^*$ is negative definite, i.e., that all eigenvalues of its symmetric part $\frac{1}{2}(\mathsf{J} + \mathsf{J}^{\mathrm{T}})$ are negative.

Remark More precisely, Leimar (2009) established that it is sufficient that J is negative definite, and necessary that it is negative semi-definite. In the borderline case any strong convergence is non-robust against arbitrary small perturbations of the model.

Negative definiteness is a strong requirement. However, it appears that most published models that describe the evolutionary dynamics of a multivariate trait by means of the adaptive dynamics approximation fulfill this criterion (Leimar 2001; Vukics et al. 2003; Ackermann and Doebeli 2004; Beltman and Metz 2005; Ito and Shimada 2007; Ravigné et al. 2009; Doebeli and Ispolatov 2010; Svardal et al. 2011, 2014). It

is therefore of some relevance to know whether for this special but apparently regularly occurring case a similar dependency exists as for one-dimensional trait spaces. We show that this is indeed to a certain extent the case: when the symmetric part of the Jacobian matrix of the fitness gradient is negative definite, condition (ii) implies conditions (iii) and (iv), so diversification at least will get started. However, it is not yet clear whether in these cases also (v) is implied. It thus remains an open problem whether for clonal reproducers strong convergence guarantees that an incipient diversification will culminate in more extended branching. The best we could do for the present is give some stronger conditions guaranteeing that such is the case.

2 Technical context

We start our treatment with a short methodological introduction. We are interested in the evolutionary dynamics of a population in which individuals are characterized by n quantitative traits. Thus, each individual is described by a trait vector $\mathbf{x} = (x_1, \ldots, x_n)^{\mathrm{T}}$. We follow the dynamics of the traits over evolutionary time as it results from repeated mutant substitutions. Specifically, we consider a simplified mutational process in a clonal population in which rare mutations of small effect change the trait values from $\mathbf{x}$ to $\mathbf{y} = \mathbf{x} + \Delta_{\mathbf{x}}$ and where mutations can occur in all directions in trait space. The evolutionary dynamics can then be determined by following a series of mutation-substitution events in which the trait vector $\mathbf{x}$ of the resident population changes over time. The fundamental tool to predict this dynamics are the invasion fitnesses $s(\mathbf{y}; \mathbf{x})$, which are defined as the expected long-term exponential growth rate of an infinitesimally small mutant subpopulation with trait vector $\mathbf{y}$ in an environment in which all relevant components such as prey, pathogen and predator densities are determined by the resident population with trait vector $\mathbf{x}$ (Metz et al. 1992; Metz 2008) (the latter revised as Metz 2014).

In the limit of rare mutation events and small unbiased mutational steps the evolutionary dynamics can be described by

$$\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = n_{\mathrm{e}}(\mathbf{x})\theta\Sigma(\mathbf{x})\mathbf{g}(\mathbf{x}) \tag{1}$$

(Dieckmann and Law 1996; Durinx et al. 2008; Metz and de Kovel 2013; Metz and Jansen, in prep). Here, $n_{\mathrm{e}}(\mathbf{x})$ is the effective population size as in population genetics, θ the mutation probability per birth event and Σ the n-dimensional mutational variance–covariance matrix summarising the distribution of mutations supposed to be symmetric around the resident type $\mathbf{x}$. Finally, $\mathbf{g}(\mathbf{x})$ denotes the n-dimensional selection gradient with entries

$$g_i(\mathbf{x}) := \left.\frac{\partial s(\mathbf{y}; \mathbf{x})}{\partial y_i}\right|_{\mathbf{y}=\mathbf{x}}. \tag{2}$$

A point $\mathbf{x}^*$ where $\mathbf{g}(\mathbf{x}^*) = 0$ is referred to as an *evolutionarily singular strategy* (*ess*). At such points the evolutionary dynamics described by Eq. (1) comes to a halt.

When mutation limitation fails, as is necessarily the case close to evolutionarily singular points, one can fall back on *Lande's equation* from quantitative genetics

Fig. 1 Output of an individual based model showing a branching trajectory without full mutation limitation. At equally spaced times a dot was drawn for each individual present at that time. Note that the standing variation of the monomorphic population and of the branches remain roughly constant except during the widening of the distribution that precedes the splitting of the branches

(modified to take account of the changes in the fitness landscape resulting from the trait evolution) which is similar to Eq. (1), except that the term $n_e(\boldsymbol{x})\theta\Sigma$ is replaced by the covariance matrix of the standing genetic variation, which we, with some slight abuse of notation, shall also denote as Σ (Lande 1979, 1982). The usual additional assumption is that Σ is constant, interpreted as approximation for the case of relatively small evolutionary change (c.f. Fig. 1). We will use this approximation when considering the initial divergence of the evolutionary branches. Of course, both the canonical and Lande's equation fail really close to the singular point when the spreading unimodal trait distribution is becoming multimodal. However, when the modes have grown sufficiently far apart their movement can initially again be modeled by a set of coupled Lande equations, that is, till the strength of directional selection in each branch increases to a level where the consumption of standing variation gets too large relative to its mutational replenishment.

Remark Three features distinguish the canonical and Lande's equation. Firstly, the stress of the canonical equation is on the change of the fitness landscape that inevitably follows in the wake of trait evolution [the part Fisher 1958 suppressed in the mathematical formulation of his fundamental theorem (p. 37), although he was obviously well aware of it (pp. 45–49)], whereas in Lande's equation, as standardly encountered, such changes are neglected. Secondly, where the canonical equation is formulated in terms of the hypothetical underlying variation generating mechanism, Lande's equation uses the empirically accessible standing genetic variation. Both differences make Lande's equation more useful for concretely describing less extensive evolutionary changes, and the canonical equation more appropriate for the theoretical consideration of larger scale changes. Thirdly, the canonical equation has been rigorously underpinned (Dieckmann and Law 1996; Champagnat 2003; Tran 2006; Durinx et al.

2008; Méléard and Tran 2009; Champagnat and Méléard 2011; Collet et al. 2013; Metz and de Kovel 2013; Metz and Jansen, in prep), albeit using a biologically seemingly unrealistic limit procedure (but see the arguments of Metz and de Kovel (2013) about its domain of validity as an approximation), whereas the heuristic underpinning of Lande's equation so far has not been subjected to such a rigorous treatment.

For a matrix M we shall use $M > 0$ ($<0, \geqslant 0, \leqslant 0$) to indicate that it is *positive (negative, positive semi-, negative semi-)* definite, i.e., $x^T M x > 0$ ($<0, \geqslant 0, \leqslant 0$) for all $x \neq 0$. In the case of non-symmetric M this means that the various kinds of definiteness are not so much properties of the full M as of its symmetric part $\frac{1}{2}(M + M^T)$, without involvement of its antisymmetric part $\frac{1}{2}(M - M^T)$.

The singular point is invadable by nearby mutants if the Hessian matrix H of the invasion fitness evaluated at x^*, with entries

$$h_{ij} := \left. \frac{\partial^2 s(y; x^*)}{\partial y_i \partial y_j} \right|_{y=x^*}, \tag{3}$$

is not negative semi-definite and only if it is not negative definite, or, equivalently, if its dominant eigenvalue λ_1 is positive and only if it is non-negative. Note that the Hessian matrix is necessarily symmetric: $h_{ij} = h_{ji}$. If $\lambda_1 > 0$, then x^* is not a local maximum of the fitness landscape but either a minimum or a saddle point and nearby mutants y that correspond to a higher point on this landscape are able to invade the population. In this case, selection is disruptive in at least some directions in trait space.

We introduce the following notation:

$$C_{00} := \frac{1}{2} \left. \frac{\partial^2 s(y; x)}{\partial y^2} \right|_{y=x=x^*}, \quad C_{10} := \frac{1}{2} \left. \frac{\partial^2 s(y; x)}{\partial x \partial y} \right|_{y=x=x^*},$$

$$C_{01} := \frac{1}{2} \left. \frac{\partial^2 s(y; x)}{\partial y \partial x} \right|_{y=x=x^*}, \quad C_{11} := \frac{1}{2} \left. \frac{\partial^2 s(y; x)}{\partial x^2} \right|_{y=x=x^*}. \tag{4}$$

Thus, $2C_{00} = H$ and $C_{01} = C_{10}^T$.

Leimar (2009) showed that a singular point is robustly asymptotically stable for any variance–covariance matrix Σ (of the mutational or standing variation) if the Jacobian matrix $J = 2(C_{00} + C_{01})$ of the selection gradient at x^* is negative definite, while Σ has an essential influence when J is not negative semi-definite. From $s(x; x) = 0$ applied to the second order term in its expansion around $x = x^*$ (in both positions) it follows that

$$C_{00} + C_{01} + C_{10} + C_{11} = 0, \tag{5}$$

which is equivalent to

$$C_{00} + \frac{C_{01} + C_{10}}{2} = -\frac{C_{01} + C_{10}}{2} - C_{11} \tag{6}$$

and therefore

$$(J + J^T)/2 < 0 \iff C_{00} + \frac{C_{01} + C_{10}}{2} < 0 \iff C_{00} - \frac{C_{00} + C_{11}}{2} < 0$$

$$\iff \frac{C_{00} - C_{11}}{2} < 0 \iff C_{11} - C_{00} > 0. \tag{7}$$

Thus, the condition for robust strong convergence stability *sensu* Leimar (2009) can be rephrased as $C_{11} - C_{00} > 0$.

3 Coexistence on the ecological time scale

For diversification to get of the ground it is necessary that close to the ess at least two phenotypes can coexist. Under certain smoothness conditions the coexistence of similar strategies is necessarily of the protected type, i.e., each phenotype can invade into the other one (Geritz, unpublished), see also (Geritz 2005; Dercole and Geritz, submitted). Therefore we start with investigating the conditions for mutual invadability near an ess. The starting point is the Taylor approximation of the invasion fitness function

$$s(x^* + v; x^* + u) = v^T C_{00} v + 2v^T C_{01} u + u^T C_{11} u + \text{h.o.t.} \tag{8}$$

To diminish verbiage we shall phrase our arguments as if the reign of the quadratic approximation of s extends forever, as is the case when we look at the geometry on the scale of the mutational steps.

The conditions for mutual invadability are

$$u_1{}^T C_{00} u_1 + 2u_1{}^T C_{01} u_2 + u_2{}^T C_{11} u_2 > 0 \tag{9a}$$

$$u_2{}^T C_{00} u_2 + 2u_2{}^T C_{01} u_1 + u_1{}^T C_{11} u_1 > 0. \tag{9b}$$

To render these inequalities in a better interpretable form we introduce $m := \frac{1}{2}(u_1 + u_2)$, the mean of the two trait vectors, and $d := \frac{1}{2}(u_1 - u_2)$, half their difference, so that $u_1 = m + d$ and $u_2 = m - d$ (Fig. 2).

Substitution of these expressions in Eq. (9) and perusing Eq. (5) gives

$$-d^T(C_{00} + C_{11})d < 2d^T(C_{10} + C_{11})m < d^T(C_{00} + C_{11})d, \tag{10}$$
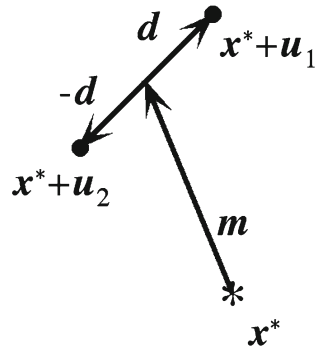
or, equivalently,

$$-d^T(C_{00} + C_{11})d < 2d^T(C_{00} + C_{01})m < d^T(C_{00} + C_{11})d, \tag{11}$$

or, equivalently,

$$d^T C_{01} d < d^T(C_{00} + C_{01})m < -d^T C_{01} d. \tag{12}$$

Equations (11), (12) imply that there exist mutually invadable trait pairs near an evolutionarily singular point if and only if there exist vectors d such that $d^T(C_{00} +$

Fig. 2 Geometrical
interpretation of the vectors m
and d

$C_{11})d > 0$, or equivalently $-d^T C_{01} d > 0$. (For the if direction take $m = 0$.) These inequalities can hold good if and only if $C_{00} + C_{11}$ has at least one positive eigenvalue, or in other words, is not negative definite.

Remark It may seem that we are a bit sloppy here as in a deterministic model a type may also invade when its invasion fitness is zero, except that it takes very long to do so. However, our deterministic models are only large system size limits of individual-based models. If the invasion fitness is zero, in the limit the probability that such a type invades, i.e., from a single individual its numbers grow to the order of magnitude of the system size, goes to zero. So in practice one can neglect this possibility, so that what in a strict mathematical sense is only a sufficient condition becomes an effectively necessary and sufficient one.

As a next step we take a closer look at the width of the $2n$-dimensional set of coexisting pairs $\mathcal{D}$, characterised by Eq. (11), as this determines the ease with which the adaptive dynamics will step from the monomorphic to a polymorphic condition. We deliberately use the word 'width' since $\mathcal{D}$ is scale-invariant, that is, $\alpha \mathcal{D} = \mathcal{D}$ for all $\alpha \in \mathbb{R}$. So what matters are the directions in $\mathbb{R}^{2n}$ that correspond to coexistence.

As a warming up we first consider the one-dimensional case. There the condition of mutual invadability reduces to

$$- (c_{00} + c_{11})d < (c_{00} - c_{11})m < (c_{00} + c_{11})d \tag{13}$$

with $m = \frac{1}{2}(u_1 + u_2)$, $d = \frac{1}{2}(u_1 - u_2)$. The simplification relative to Eq. (11) derives from the fact that in the scalar case $c_{ij} = c_{ji}$ so that $2(c_{00} + c_{01}) = c_{00} + c_{01} - c_{10} - c_{11} = c_{00} - c_{11}$. In a mutual invadability plot as depicted in Fig. 3, $\sqrt{2}d$ equals the distance of (u_1, u_2) to the diagonal, and $\sqrt{2}m$ the distance to the anti-diagonal through x^*. For singular points that are both attracting and invadable the coexistence cone always has a width of more than 90°, and is symmetric around the diagonal as well as the anti-diagonal.

As in the one-dimensional case, generally the pair (m, m) can be interpreted as the orthogonal projection of (u_1, u_2) on the linear manifold given by $u_1 = u_2$, and $(d, -d)$ as the difference of (u_1, u_2) and that projection. In a similar vein, the symmetry of $\mathcal{D}$ around the diagonal extends to symmetry in the d directions around $d = 0$ and

Fig. 3 How the quantities d and m relate to the coexistence region (*grey*) in the mutual invadability plot of u_1 and u_2
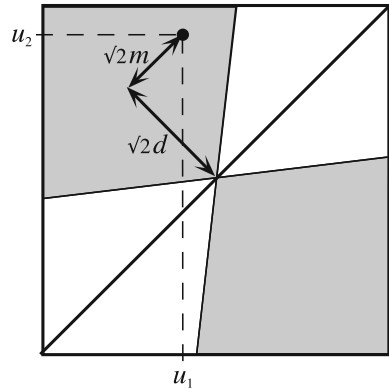
symmetry over the anti-diagonal extends to symmetry in the m directions around $m = 0$.

The one-dimensional case also can be found embedded in the n-dimensional case in the form of pairs (u_1, u_2) for which the line through u_1 and u_2 passes through the origin (situated at x^*), so that we can write $u_1 = u_1 r$ and $u_2 = u_2 r$, giving $c_{ij} = r^T C_{ij} r$.

Even when $C_{00} + C_{11}$ has only one positive eigenvalue κ_1 with eigenvector k_1, there is no need for d to be aligned with k_1 for a pair (u_1, u_2) to lie in $\mathcal{D}$. If we express d in a basis of eigenvectors, normalised such that $k_i^T k_i = 1$, all that is needed is $-\sum_2^n \kappa_i d_i^2 < \kappa_1 d_1^2$. We shall refer to d such that $d^T(C_{00} + C_{11})d > 0$ as 'allowable'. Shifting both members of a pair (u_1, u_2) in any direction orthogonal to $d(C_{00} + C_{01})$ does not affect either d or $d^T(C_{00} + C_{01})m$. Hence, to construct the set of all m that go with a certain allowable d we can start from $m = \alpha h$ with $h^T := 2d^T(C_{00} + C_{01})$ and α delimited by $-d^T(C_{00} + C_{11})d < h^T h\alpha < d^T(C_{00} + C_{11})d$, and add to these any m' orthogonal to h.

The upshot is that even when $C_{00} + C_{11}$ has only one positive eigenvalue, there are such a good amount of mutually invadable pairs that the step from mono- to dimorphism will occur rather sooner than later.

When x^* is strongly attracting $C_{11} - C_{00} > 0$. Hence, when $r^T C_{00} r > 0$ for some vectors r, also $r^T C_{11} r > 0$ and hence $r^T(C_{00} + C_{11})r > 0$. Therefore, for a strongly attracting ess invadability implies the existence of a multitude of close by mutually invadable pairs of trait vectors, of which we will see in the next section that they undergo disruptive selection, i.e., selective pressures on each member of the pair that drive them further apart.

4 Coexistence on the evolutionary time scale

At a branching point the trait vectors representative for each of the incipient branches are subject to disruptive selection, letting them grow apart at least initially. We will follow this movement only within the reign of the quadratic approximation of the invasion fitness function close to the ess, and will do so under the assumption that the

movement is adequately represented by coupled Lande equations. (Note that with a quadratic approximation we do not mean a Taylor approximation, as the latter is only applicable when the number of coexisting trait vectors equals the dimension of the trait space (n) plus one, see below.)

We shall below again phrase our arguments as if the reign of the quadratic approximation of s extends forever. Moreover, we without further ado proceed on the assumption that coexistence results derived for the case of full mutation limitation extend to any well separated quasi-monomorphic clusters that replace the single phenotypes when there is less than strict mutation limitation. Lastly, we will adapt the coordinate system so as to transform Σ into the identity matrix.

Other than perhaps expected from the scalar case, in the multivariate case there is the possibility for $h > 2$ phenotypes to coexist near an ess. (The reason why we have not gone into this potential complication in the previous section will become clear further on.) If the demographic parameters of the individuals under consideration depend smoothly on their phenotype then s will depend smoothly on the mutant trait vector $\boldsymbol{v}$ (Ferrière and Gatto 1995). Such smoothness cannot be assumed for the dependence on $(\boldsymbol{u}_1, \ldots, \boldsymbol{u}_h)$ since the environment created by the residents $(\boldsymbol{x}^* + \boldsymbol{u}_1, \ldots, \boldsymbol{x}^* + \boldsymbol{u}_h)$ is determined by the attractor of their community dynamics. Assuming smoothness in the resident phenotype for monomorphisms is pretty harmless, as at least for simple community attractors this is guaranteed away from community dynamical bifurcation points by some form of the inverse function theorem. This argument extends to polymorphisms, but not necessarily to the boundary of the region in $\mathbb{R}^{hn}$ harbouring h-morphisms, as these are characterised by the occurrence of a bifurcation. In particular at corners of that boundary, like the point $(\boldsymbol{x}^*, \ldots, \boldsymbol{x}^*) \in \mathbb{R}^{hn}$, differentiability can fail. Hence, we may expect the dependence of s on $(\boldsymbol{u}_1, \ldots, \boldsymbol{u}_h)$ to have at best directional derivatives, but generally not to have a full derivative. An argument, in terms of the local geometry of the community dynamics, why directional derivatives can still be expected to exist can be found in (Durinx et al. 2008).

The Taylor expandability of s in $\boldsymbol{v}$ gives

$$s(\boldsymbol{x}^* + \boldsymbol{v}; \boldsymbol{x}^* + \boldsymbol{u}_1, \ldots, \boldsymbol{x}^* + \boldsymbol{u}_h) = a + \boldsymbol{b}^{\mathrm{T}}\boldsymbol{v} + \boldsymbol{v}^{\mathrm{T}}\mathsf{C}_{00}\boldsymbol{v}, \qquad (14)$$

with a and $\boldsymbol{b}$ functions of $(\boldsymbol{u}_1, \ldots, \boldsymbol{u}_h)$, which we take to be second and first order respectively (on the strength of the existence of the directional derivatives). The explicit expression for the quadratic term is found from the ecological consistency condition

$$s(\boldsymbol{x}^* + \boldsymbol{v}; \boldsymbol{x}^*, \ldots, \boldsymbol{x}^*) = s(\boldsymbol{x}^* + \boldsymbol{v}; \boldsymbol{x}^*). \qquad (15)$$

One first result from the other ecological consistency conditions

$$s(\boldsymbol{x}^* + \boldsymbol{u}_i; \boldsymbol{x}^* + \boldsymbol{u}_1, \ldots, \boldsymbol{x}^* + \boldsymbol{u}_h) = 0, \quad \text{for } i = 1, \ldots, h, \qquad (16)$$

is that close to $\boldsymbol{x}^*$ generically at most $n + 1$ phenotypes can coexist, as otherwise the number of equations for a and the components of $\boldsymbol{b}$ exceeds the number of unknowns, a result going back to Christiansen and Loeschke (1987). When the number of coexisting phenotypes equals $n + 1$, Eqs. (15) and (16) fully determine s. When the number of

phenotypes is less than $n + 1$ this is no longer the case and it becomes necessary to proceed through the harrowing procedure of calculating s from first principles. Luckily, there are still some results to be derived in a more lazy manner.

Our primary interest at this point is not s itself, but the selection gradients

$$g_i^T(u_1, \ldots, u_h) := \frac{\partial s(v; u_1, \ldots, u_h)}{\partial v}\bigg|_{v=u_i} = b^T(u_1, \ldots, u_h) + 2C_{00}u_i. \quad (17)$$

The form of Eq. (17) suggests defining $m := h^{-1}(u_1 + \cdots + u_h)$ and $d_i := u_i - m$, which when substituted in the Lande equations yields

$$\frac{dd_i}{dt} = 2C_{00}d_i. \quad (18)$$

Hence, all d_i will in the long run align in a direction parallel to the eigenvector z corresponding to the dominant eigenvalue λ_1 of $H = 2C_{00}$, which we assume to be unique and positive. As a result all u_i will get to lie at any given large time close to a single line $\{m + \zeta z | \zeta \in \mathbb{R}\}$. Restricted to such a line s becomes a quadratic function of ζ. In combination with the consistency relation Eq. (16) this implies the following result:

Proposition *Generically, expanding polymorphisms around ess-es initially evolve towards becoming dimorphisms.*

For dimorphisms, under the assumption that the community dynamics converges to an equilibrium point

$$s(v; u_1, u_2) = m^T C_{11} m - d^T C_{00} d + v^T C_{00} v$$
$$+ 2\left(m^T C_{10} v - \frac{d^T(C_{00} + C_{01})m}{d^T C_{01} d} d^T C_{10}(v - m)\right) \quad (19)$$

with $d = d_1 = -d_2$ (Durinx et al. 2008), which in the univariate case (for which $n + 1 = 2$) reduces to

$$s(v; u_1, u_2) = c_{00}(v - u_1)(v - u_2) \quad (20)$$

To see what can be deduced from Eq. (19) about the longer term coexistence of the diverging branches we calculate the selection gradients

$$g_i(u_1, u_2) = 2\left(C_{01} m - \frac{d^T(C_{00} + C_{01})m}{d^T C_{01} d} C_{01} d\right) + 2C_{00}u_i, \quad (21)$$

which in the univariate case reduce to

$$g_1(u_1, u_2) = c_{00}(u_1 - u_2), \quad g_2(u_1, u_2) = c_{00}(u_2 - u_1). \quad (22)$$

Therefore the answer for the univariate case is easy. Since $\mathrm{d}d/\mathrm{d}t = 2c_{00}d$ and $\mathrm{d}m/\mathrm{d}t = 0$, the dimorphism generated at a branching point will just expand over evolutionary time. In the multivariate case we get

$$\frac{\mathrm{d}\boldsymbol{d}}{\mathrm{d}t} = 2\mathsf{C}_{00}\boldsymbol{d}, \tag{23a}$$

$$\frac{\mathrm{d}\boldsymbol{m}}{\mathrm{d}t} = 2\left(\mathsf{C}_{01}\boldsymbol{m} - \frac{\boldsymbol{d}^{\mathrm{T}}(\mathsf{C}_{00} + \mathsf{C}_{01})\boldsymbol{m}}{\boldsymbol{d}^{\mathrm{T}}\mathsf{C}_{01}\boldsymbol{d}}\mathsf{C}_{01}\boldsymbol{d}\right) + 2\mathsf{C}_{00}\boldsymbol{m}$$

$$= 2\left(\mathsf{id} - \frac{1}{\boldsymbol{d}^{\mathrm{T}}\mathsf{C}_{01}\boldsymbol{d}}\mathsf{C}_{01}\boldsymbol{d}\boldsymbol{d}^{\mathrm{T}}\right)(\mathsf{C}_{00} + \mathsf{C}_{01})\boldsymbol{m}, \tag{23b}$$

with id the identity matrix.

Given the simple form of the mutual invadability results for strongly attracting ess-es on the community dynamical time scale, the obvious next step seems to be to look under what conditions the vector field specified by Eq. (23) points towards the interior of $\mathcal{D}$ at points on its boundary. This amounts to seeing whether the scalar functions $\boldsymbol{d}^{\mathrm{T}}\mathsf{C}_{01}\boldsymbol{d} - \boldsymbol{d}^{\mathrm{T}}(\mathsf{C}_{00} + \mathsf{C}_{01})\boldsymbol{m}$ and $\boldsymbol{d}^{\mathrm{T}}\mathsf{C}_{01}\boldsymbol{d} + \boldsymbol{d}^{\mathrm{T}}(\mathsf{C}_{00} + \mathsf{C}_{01})\boldsymbol{m}$ are bound to increase from their zero values. However, the expressions for the time derivatives of these functions, although simple looking, do not give any clear clues.

The next step is again to look at the large time behaviour of the solutions of Eq. (23).

In the case of (23a),

$$\boldsymbol{d}(t) \approx c\mathrm{e}^{\lambda_1 t}\boldsymbol{z}. \tag{24}$$

From Eqs. (12) and (24) it follows that in the longer run branching can only persist if

$$2\boldsymbol{z}^{\mathrm{T}}\mathsf{C}_{01}\boldsymbol{z} = -\boldsymbol{z}^{\mathrm{T}}(\mathsf{C}_{00} + \mathsf{C}_{11})\boldsymbol{z} < 0. \tag{25}$$

(as is the case for strongly attracting ess-es). As we are interested only in cases with non-empty coexistence cone we proceed on the assumption that Inequality (25) holds good.

From Eq. (23b) it moreover follows that

$$\boldsymbol{d}^{\mathrm{T}}\frac{\mathrm{d}\boldsymbol{m}}{\mathrm{d}t} = 0. \tag{26}$$

Hence, in the long run $\boldsymbol{m}$ either stays bounded, and therefore becomes negligible relative to $\boldsymbol{d}$, or becomes orthogonal to $\boldsymbol{z}$.

To simplify the coming formulas we normalise $\boldsymbol{z}$ such that $\boldsymbol{z}^{\mathrm{T}}\mathsf{C}_{01}\boldsymbol{z} = -1$. Substituting Eq. (24) in the differential equation for $\boldsymbol{m}$ then gives

$$\frac{\mathrm{d}\boldsymbol{m}}{\mathrm{d}t} \approx 2(\mathsf{id} + \mathsf{C}_{01}\boldsymbol{z}\boldsymbol{z}^{\mathrm{T}})(\mathsf{C}_{00} + \mathsf{C}_{01})\boldsymbol{m}. \tag{27}$$

In view of Eq. (26) the matrix $2(\mathsf{id} + \mathsf{C}_{01}\boldsymbol{z}\boldsymbol{z}^{\mathrm{T}})(\mathsf{C}_{00} + \mathsf{C}_{01})$ has an eigenvalue 0, and the eigenvectors corresponding to the other eigenvalues are orthogonal to $\boldsymbol{z}$. Denote the

largest eigenvalue of $2(\mathsf{id}+\mathsf{C}_{01}zz^{\mathrm{T}})(\mathsf{C}_{00}+\mathsf{C}_{01})$ with eigenvector w in the latter class as μ_1. (We assume here that this eigenvalue is real. The extension of the argument to a pair of complex eigenvalues is immediate but tedious.) For the inequalities (11) to stay fulfilled

$$\mathrm{e}^{-2\lambda_1 t}d^{\mathrm{T}}(\mathsf{C}_{00}+\mathsf{C}_{01})m \asymp \mathrm{e}^{(\mu_1-\lambda_1)t}z^{\mathrm{T}}(\mathsf{C}_{00}+\mathsf{C}_{01})w = \mathrm{e}^{(\mu_1-\lambda_1)t}z^{\mathrm{T}}\mathsf{C}_{01}w \quad (28)$$

($\asymp$: is asymptotically proportional to) should not grow out of bounds. Moreover, when the expressions in (28) stay bounded, for sufficiently small initial m the inequalities (11) stay fulfilled.

A sufficient condition for the expressions in (28) to stay bounded is that $\lambda_1 > \mu_1$. This condition is also necessary when $z^{\mathrm{T}}\mathsf{C}_{01}w \neq 0$. The condition $z^{\mathrm{T}}\mathsf{C}_{01}w = 0$ together with the earlier found relations is equivalent to $2\mathsf{C}_{00}z = \lambda_1 z$, $2(\mathsf{C}_{00}+\mathsf{C}_{01})w = \mu_1 w$, $z^{\mathrm{T}}w = 0$. Although this of course depends on the considered model family, the fullfilment of these three conditions together in general is highly non-generic. Hence, generally the conditions

$$z^{\mathrm{T}}\mathsf{C}_{01}z \leqslant 0 \quad \& \quad \lambda_1 > \mu_1 \quad (29)$$

are generically necessary and sufficient to make that for a sufficiently small initial value of m the two branches remain coexistent at least within the reign of the local quadratic approximation of the invasion fitness function.

Remark The above considerations also apply when dealing with more than one evolving species. However, in the one-species case considered in this paper, it is possible to make the stronger argument that $2(\mathsf{C}_{00}+\mathsf{C}_{01}) = \mathsf{J}$. As it only makes sense to consider branching at attracting singular points, J may be supposed to have only eigenvalues with negative real parts. Hence when $z^{\mathrm{T}}\mathsf{C}_{01}w = 0$, anyway $\lambda_1 > \mu_1$.

So far we have been unable to find an example of an invadable strongly attracting ess that fails to satisfy (29), but neither have we been able to prove that such ess-es do not exist. *So we flag the question whether strong attraction and invadability together imply locally sustainable branching as open problem.* The next section describes the results in this direction that we could obtain under various additional assumptions.

5 Special cases

In this section we consider a number of special cases for which we could get more information about the possible occurrence of locally unsustainable branching.

We start with the case of 2-dimensional trait spaces. As a first step we observe that for such trait spaces we can without loss of generality assume that

$$\mathsf{C}_{00} = \frac{1}{2}\begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}, \quad \mathsf{C}_{01} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}, \quad (30)$$

with $a < 0$ to guarantee the existence of a coexistence cone. (The form (30) can be reached by choosing the normalised eigenvectors of C_{00} as new orthogonal coordinate

system. The resulting transformation of the matrices C_{ij} does not affect λ_1 or μ_1.)
This then gives

$$z = \begin{pmatrix} 1/\sqrt{-a} \\ 0 \end{pmatrix}. \tag{31}$$

μ_1 is the only nonzero eigenvalue of

$$\left[\text{id} + \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} -a^{-1} & 0 \\ 0 & 0 \end{pmatrix} \right] \left[\begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix} + 2 \begin{pmatrix} a & b \\ c & d \end{pmatrix} \right]$$

$$= \begin{pmatrix} 0 & 0 \\ -a^{-1}c\lambda_1 & \lambda_2 + 2a^{-1}(ad - bc) \end{pmatrix}, \tag{32}$$

$\lambda_2 + 2a^{-1}(ad - bc)$. Hence, the expansion of d dominates, and the expanding branches can stay in the coexistence cone if

$$\lambda_1 - \lambda_2 - 2a^{-1}(ad - bc) > 0, \tag{33}$$

and only if (33) holds good with $>$ replaced, by $\geqslant$.

As it turns out (33) is implied by the requirement that the ess x^* attracts for the chosen mutational or genetic covariance matrix. (Remember, λ_1, λ_2, a, b, c and d where obtained from the original matrices C_{00} and C_{01} by a change of basis that transformed Σ into id.) The attractivity of x^* is determined by $J = 2(C_{00} + C_{01})$. If and only if the eigenvalues of J have non-positive real part x^* attracts. This is robustly the case if and only if

$$\text{trace}(J) = \lambda_1 + \lambda_2 + 2a + 2d < 0 \ \ \& \ \ \det(J) = (\lambda_1 + 2a)(\lambda_2 + 2d) - 4bc > 0 \tag{34}$$

With the help of the functions `Reduce` and `FindInstance` in *Mathematica* (Wolfram Research, Inc.) we found that the Inequalities (34) imply (33). Hence, *locally unsustainable branching cannot occur in 2-dimensional trait spaces*.

By following a similar procedure we found instances of locally unsustainable branching in three dimensions (see Appendix). However, when we concentrated on strongly attracting ess-es *Mathematica* failed to resolve the issue.

As we have so far not been able to clarify whether in general strong attractivity guarantees $\lambda_1 > \mu_1$, we went for potentially useful more stringent conditions.

Proposition *Assume that a coordinate system of the trait space exists such that both* C_{00} *and* C_{01} *are diagonal matrices with diagonal entries* p_{ii} *and* q_{ii}, *respectively. Furthermore, assume* C_{00} *has a unique largest positive diagonal entry equal to* p_{11} *and* $p_{ii} + q_{ii} < 0$ *for all* i. *Then* $\mu_1 < 0$.

Proof Normalize the eigenvector z corresponding to the dominant eigenvalue of C_{00} such that $z^T C_{01} z = -1$. Then it is easy to see that $M := C_{01} z z^T$ has $m_{11} = -1$ and zeros elsewhere. Hence, $K := (\text{id} + C_{01} z z^T)(C_{00} + C_{01})$ is a diagonal matrix with $k_{11} = 0$ and $k_{ii} = p_{ii} + q_{ii}$ for $i > 1$. $\qquad\square$

Since by assumption $\lambda_1 > 0$, the conditions of this proposition imply $\lambda_1 > \mu_1$. They are fulfilled in the Lotka–Volterra models studied by Ackermann and Doebeli (2004), Doebeli and Ispolatov (2010) and Svardal et al. (2014).

6 Discussion

The evolutionarily singular strategies of published eco-evolutionary models with multivariate traits often turn out to be strongly attracting (i.e., robustly convergence stable *sensu* Leimar 2009). Under the assumption that the latter is the case we established that for the initiation of evolutionary branching it suffices that the ess is invadable. In several published studies this has been tacitly assumed, based on the hope that the classical results for one-dimensional trait spaces extend unmodified to the multi-dimensional case. We thus proved that this is indeed the case for the initiation of branching, but unfortunately we were not able to prove that under the same conditions a similar statement holds true for its continuation at least within the realm of a quadratic expansion of the invasion fitness function for the dimorphism. To arrive at these results we analysed the geometry of mutual invadability around general multivariate ess-es. This gave the initial positive result. Next we derived criteria for checking whether the initial mutual invadability extends to the expanding dimorphisms that ensue from disruptive selection. However, here we could not make a link with the negative definiteness of the Jacobian matrix of the monomorphic selection gradient at the ess (the signature of strong attractivity) due to the cross-derivatives in the Taylor expansion of the monomorphic invasion fitness function turning up in the dimorphic selection gradients. Hence, whether a branching point indeed spawns temporarily persisting branches on the evolutionary time scale is a question which in general requires separate investigation. The relations between the five conditions for branching, (i) attraction, (ii) invadability, (iii) nearby population dynamical coexistence, (iv) nearby disruptive selection, (v) nearby evolutionary coexistence, given in the introduction thus become: conditions (i) and (ii) are independent, (iii) is implied by (i) and (ii) in the strongly convergent stable case (which includes the case of one-dimensional trait spaces), but in general is independent, (ii) and (iii) always imply (iv), finally (iii) is necessary for (v) but not sufficient, except when the trait space is one- or two-dimensional. However, we were unable to resolve whether in the strongly convergent stable case (iii) implies (v). The best we could do here was to give some appreciably stronger conditions under which the latter implication holds good. Finally, and perhaps biologically most relevantly, we established that, within the reign of the local quadratic approximation of the fitness function, expanding polymorphisms around ess-es in general initially evolve towards (quasi)-dimorphisms, or after a short while fall back to (quasi)-monomorphism (which in case the ess attracts will again lead to an expanding polymorphism in an ever ongoing cycle).

Appendix: 3-dimensional trait spaces

The case of 3-dimensional trait spaces proceeds analogous to that of 2-dimensional trait spaces in Sect. 5. Let $\theta_i := \frac{1}{2}\lambda_i$ and $\kappa_i = \frac{1}{2}\mu_i$, and

$$
\mathsf{C}_{00} := \begin{pmatrix} \theta_1 & 0 & 0 \\ 0 & \theta_2 & 0 \\ 0 & 0 & \theta_3 \end{pmatrix}, \quad \mathsf{C}_{01} := \begin{pmatrix} p & q & r \\ u & v & w \\ x & y & z \end{pmatrix},
$$

with $p < 0$ to guarantee the local existence of a coexistence cone. The Jacobian matrix of the selection gradient at x^* then becomes

$$
\mathsf{J} = 2 \begin{pmatrix} p + \theta_1 & q & r \\ u & v + \theta_2 & w \\ x & y & z + \theta_3 \end{pmatrix}.
$$

For x^* to attract, all eigenvalues of J should have negative real part. The Routh–Hurwitz criteria tell that this is the case if and only if

$$
(i)\ a_1 = -\mathrm{trace}\left(\frac{1}{2}\mathsf{J}\right) > 0 \ \&\ (ii)\ a_3 = -\mathrm{det}\left(\frac{1}{2}\mathsf{J}\right) > 0 \ \&\ (iii)\ a_1 a_2 > a_3,
$$

where a_1 to a_3 are the coefficients of the characteristic polynomial $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$ of $\frac{1}{2}\mathsf{J}$. These inequalities evaluate to

(i) $p + v + z + \theta_1 + \theta_2 + \theta_3 < 0$

(ii) $pvz + qwx + ruy - pwy - quz - rvx + vz\theta_1 - wy\theta_1 + pz\theta_2$
$\quad - rx\theta_2 + pv\theta_3 - qu\theta_3 + z\theta_1\theta_2 + p\theta_2\theta_3 + v\theta_1\theta_3 + \theta_1\theta_2\theta_3 < 0$

(iii) $(p + \theta_1)^2(v + \theta_2) + (p + \theta_1)(v + \theta_2)^2 + (p + \theta_1)^2(z + \theta_3) + (p + \theta_1)$
$\quad (z + \theta_3)^2 + (v + \theta_2)^2(z + \theta_3) + (v + \theta_2)(z + \theta_3)^2 + 2(p + \theta_1)(v + \theta_2)$
$\quad (z + \theta_3) < qwx + ruy + qu(p + \theta_1 + v + \theta_2) + rx(p + \theta_1 + z + \theta_3)$
$\quad + wy(v + \theta_2 + z + \theta_3).$

Criteria for the strong attraction of x^* can be derived by applying the Routh–Hurwitz criteria to

$$
\frac{1}{2}\left(\mathsf{J} + \mathsf{J}^\mathsf{T}\right) = \begin{pmatrix} 2(p + \theta_1) & (q + u) & (r + x) \\ (q + u) & 2(v + \theta_2) & (w + y) \\ (r + x) & (w + y) & 2(z + \theta_3) \end{pmatrix},
$$

which results in

(i) $p + v + z + \theta_1 + \theta_2 + \theta_3 < 0$

(ii) $4(p + \theta_1)(v + \theta_2)(z + \theta_3) + (q + u)(w + y)(r + x)$
$\quad - (w + y)^2(p + \theta_1) - (r + x)^2(v + \theta_2) - (q + u)^2(z + \theta_3) < 0$

(iii) $4[2(p + \theta_1)(v + \theta_2)(z + \theta_3) + (p + \theta_1)^2(v + \theta_2) + (p + \theta_1)^2(z + \theta_3)$

$\quad + (p + \theta_1)(v + \theta_2)^2 + (p + \theta_1)(z + \theta_3)^2 + (v + \theta_2)^2(z + \theta_3) + (v + \theta_2)$

$\quad (z + \theta_3)^2] < (q + u)(w + y)(r + x) + (r + x)^2(p + \theta_1) + (q + u)^2(p + \theta_1)$

$\quad + (w + y)^2(v + \theta_2) + (q + u)^2(v + \theta_2) + (w + y)^2(z + \theta_3)$

$\quad + (r + x)^2(z + \theta_3).$

The conditions for locally sustainable branching are that the eigenvalues of

$$\left[\mathrm{id} + \begin{pmatrix} p & q & r \\ u & v & w \\ x & y & z \end{pmatrix} \begin{pmatrix} -p^{-1} & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \right] \begin{pmatrix} \theta_1 + p & q & r \\ u & \theta_2 + v & w \\ x & y & \theta_3 + z \end{pmatrix} - \theta_1 \mathrm{id}$$

$$= \begin{pmatrix} -\theta_1 & 0 & 0 \\ -u\theta_1/p & \theta_2 - \theta_1 + v - uq/p & w - ur/p \\ -x\theta_1/p & y - xq/p & \theta_3 - \theta_1 + z - xr/p \end{pmatrix}$$

have negative real part. (Rationale: The real part of the rightmost eigenvalue κ_1 of $\mathsf{K} := (\mathrm{id} + \mathsf{C}_{01}zz^{\mathsf{T}})(\mathsf{C}_{00} + \mathsf{C}_{01})$ should be smaller than θ_1. The eigenvalues of $\mathsf{K} - \theta_1 \mathrm{id}$ equal $\kappa_i - \theta_1$. So the statement above is equivalent to $\mathrm{Re}(\kappa_i - \theta_1) < 0$ for all i.) This is the case if and only if the trace of

$$\begin{pmatrix} \theta_2 - \theta_1 + v - uq/p & w - ur/p \\ y - xq/p & \theta_3 - \theta_1 + z - xr/p \end{pmatrix}$$

is negative and the determinant is positive. This can be written as

$$p(2\theta_1 - \theta_2 - \theta_3) + qu + rx - pv - pz < 0$$

and

$$p(\theta_1 - \theta_2)(\theta_1 - \theta_3) + (rx - pz)(\theta_1 - \theta_2) + (qu - pv)(\theta_1 - \theta_3)$$
$$+ p(vz - wy) + q(wx - uz) + r(uy - vx) < 0.$$

Finding cases where x^* attracts and the branching is either locally sustainable or not, using a mixture of inspired guesses with a little help from *Mathematica* (Wolfram Research, Inc.), turned out not to be too difficult. However, in the case where x^* strongly attracts both *Mathematica* and we were unable to resolve the inequalities.

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