Evolutionary Ecology Research, 2006, **8**: 959–973

Trade-off geometries and the adaptive dynamics of two co-evolving species

Éva Kisdi*

Department of Mathematics and Statistics, University of Helsinki, FIN-00014 Helsinki, Finland

ABSTRACT

Background: A recently developed geometric method makes it possible to explore how the shape of a trade-off determines the outcome of adaptive evolution in any complex model and without committing to a particular functional form of the trade-off function.

Aim: Extend the method to the co-evolution of two species. (The two species may be distantly related such as a predator and its prey, or may be closely related like two strategies produced by evolutionary branching.)

Results: Thresholds of the local convexity of the trade-off functions are obtained that guarantee evolutionary and convergence stability when a given species pair is singular. In contrast to the single-species case, the condition for convergence is sufficient but not necessary. Criteria for evolutionary branching generalize from the single-species case. A cross-derivative of the invasion fitness determines whether evolutionary branching is possible; this quantity is independent of the trade-offs and if it is negative at a certain species pair, then the trade-offs can be chosen such that evolutionary branching occurs at this point.

Worked example: A simple predator–prey model shows how these results can be used to identify trade-off functions such that evolution leads to an evolutionarily stable species pair or to evolutionary branching in either species.

Keywords: adaptive dynamics, co-evolution, critical function analysis, evolutionary branching, evolutionarily stable strategy, geometric analysis, predator–prey system, trade-off.

INTRODUCTION

'Darwinian demons', organisms that produce huge numbers of offspring, mature instantaneously, live extremely long, and do this in any environment they encounter, have not taken over the Earth because improvements in certain traits can often be bought only at some costs in others. Trade-offs are thus central to our understanding of evolutionary ecology, and part of most models of phenotypic adaptation. Classic life-history theory pioneered the study of trade-offs between growth and reproduction, between the number and size of offspring, between reproductive effort and parental survival, and between early and late reproduction (Roff, 1992). Other examples include trade-offs between fitness in two contrasting

* e-mail: eva.kisdi@helsinki.fi
Consult the copyright statement on the inside front cover for non-commercial copying policies.

© 2006 Éva Kisdi

environments, between the ability to exploit different resources, between foraging activity and predation risk, between guarding mates and steeling fertilization, and many others.

The existence of many trade-offs is empirically well documented. The shape of these trade-offs is, however, uncertain and ostensibly hard to obtain empirically; modellers can thus hardly rely on empirical data when assuming specific shapes for the trade-off functions. In a few cases, the trade-off reflects a simple stoichiometric relationship between the traits (e.g. the fractions of dispersed and of philopatric offspring must add up to one; the sum of investments into male and female offspring equals the total investment available for reproduction), and this relationship determines the shape of the trade-off. But even the apparently straightforward trade-off between the number and size of offspring may be considerably more complex than just allocating a fixed total investment R among n offspring of size R/n (Fischer *et al.*, 2006).

Postulating a particular shape for a trade-off function is often the least justified assumption of the model. This is of serious concern because by restricting attention to a specific functional form of the trade-off (and varying only the parameters of the chosen trade-off function), some possible evolutionary outcomes may be missed (see examples in de Mazancourt and Dieckmann, 2004; Geritz *et al.*, submitted).

Based on Levins' (1962, 1968) fitness set approach, recently there has been interest in developing a geometrical method of analysis where the shape of the trade-off does not have to be specified beforehand (de Mazancourt and Dieckmann, 2004; Rueffler *et al.*, 2004; Bowers *et al.*, 2005; see Geritz *et al.*, submitted, for an application). This new method is applicable to a wide class of models with frequency-dependent selection, and has been explicitly linked to adaptive dynamics (*sensu* Geritz *et al.*, 1998). Instead of supposing a particular trade-off function and then working out the expected dynamics of evolution, the new method derives a family of curves that can be quickly compared with any trade-off function in the last step of the analysis, in order to see how evolution proceeds under various trade-offs. The analytic properties of these curves, here called *critical functions*, constrain the properties of trade-offs that result in one or another evolutionary outcome. Critical functions can be obtained numerically also in complex models.

To date, this new method has been available only for analysing evolution in monomorphic populations of a single species. In many instances, however, we are concerned with the co-evolution of two unrelated species such as a predator and its prey, or a host and its parasite. Even in a single species, frequency-dependent selection may lead to evolutionary branching (Geritz *et al.*, 1998), whereby two distinct types, henceforth called 'strategies', evolve in the population. The two strategies could represent closely related species (if reproductive isolation evolves), or within-species diversity such as genetic polymorphism (Kisdi and Geritz, 1999) or sexual dimorphism (Bolnick and Doebeli, 2003; Van Dooren *et al.*, 2004). When a model predicts the possibility of branching, one would naturally like to follow the co-evolution of the two emerging strategies and determine whether they attain an evolutionarily stable co-existence or, for example, further diversification takes place.

The extension of critical function analysis to polymorphic populations or to systems with multiple species is not straightforward (de Mazancourt and Dieckmann, 2004). Of the two central concepts of adaptive dynamics, evolutionary stability (i.e. whether a strategy or a co-existence of strategies is immune against invasion by new mutants) generalizes directly from monomorphic to polymorphic populations (Geritz *et al.*, 1998; Rueffler *et al.*, 2004). Convergence stability (i.e. whether a singular strategy is attainable by small evolutionary steps), however, does not extend easily to higher dimensions. In particular, convergence

stability may depend on the relative speed of evolution in the co-evolving species or strategies, as determined by the frequency and size of mutations (Dieckmann and Law, 1996; Marrow *et al.*, 1996; Matessi and Di Pasquale, 1996; Leimar, in press).

In this paper, I partially extend the method of de Mazancourt and Dieckmann (2004) to populations that contain two co-evolving species or strategies. Building on the results of Matessi and Di Pasquale (1996), I derive a sufficient (but not necessary) condition for convergence stability in terms of the convexity of the trade-off functions. Combining this result with the (necessary and sufficient) condition for evolutionary stability, I show that co-evolution leads to an evolutionarily stable co-existence whenever the trade-offs are sufficiently concave. I also investigate the conditions under which a species or strategy may undergo further evolutionary branching.

EVOLUTION SUBJECT TO A TRADE-OFF IN MONOMORPHIC POPULATIONS

Before turning to co-evolution of two species or strategies, I briefly review the connection between trade-off geometries and adaptive dynamics in monomorphic populations of a single species based on the results of de Mazancourt and Dieckmann (2004; see also Rueffler *et al.*, 2004; Bowers *et al.*, 2005). The necessary background of adaptive dynamics can be found in Geritz *et al.* (1998).

Assume that fitness is a strictly monotonic function of a trait y and of another trait z that is traded off with y such that $z = f(y)$, where f is a twice continuously differentiable function. In a resident population with strategy x, the invasion fitness of mutant y can be written in the form

$$s_x(y) = \tilde{s}(y, f(y), x, f(x)) \tag{1}$$

I shall denote the derivatives of $\tilde{s}$ by subscripts (e.g. $\tilde{s}_1 = \partial\tilde{s}/\partial y$, $\tilde{s}_{13} = \partial^2\tilde{s}/\partial y\partial x$). Without loss of generality, I assume that $\tilde{s}$ is increasing in its second argument ($\tilde{s}_2 > 0$). Note that the invasion fitness in equation (1) can encompass a complex ecological system with frequency-dependent selection (Metz *et al.*, 1992). I assume, however, that traits y and z are heritable individual traits such that the trade-off between them is due to the physiology of the individual, i.e. the shape of $z = f(y)$ is not affected by the population or by the environment. As usual in adaptive dynamics, I assume that mutations have small phenotypic effects.

By repeated mutations and substitutions, the population evolves in the direction of the fitness gradient $[\partial s/\partial y]_{y=x} = \tilde{s}_1 + \tilde{s}_2 f'(x)$. A certain strategy $(x^*, f(x^*))$ is singular if the fitness gradient at x^* is zero, i.e. if

$$f'(x^*) = -\tilde{s}_1/\tilde{s}_2 \tag{2}$$

where the derivatives of $\tilde{s}$ are evaluated at $(x^*, f(x^*), x^*, f(x^*))$.

A curve that has the slope given by equation (2) at *every* point $(x, f(x))$ is called an A-boundary by de Mazancourt and Dieckmann (2004); I refer to such a curve as a critical function. A critical function $\varphi(x)$ is thus a solution of the differential equation

$$\varphi'(x) = -\tilde{s}_1(x, f(x), x, f(x))/\tilde{s}_2(x, f(x), x, f(x)) \tag{3}$$

and the solutions with different initial values form a family of critical functions.

Critical functions belonging to various initial points can be plotted by solving equation (3); numerical solutions can easily be obtained even in complex models. From the definition, it is clear that singular strategies are those points where the trade-off function $f(x)$ is tangential to a critical function, because at the points of tangent the trade-off function has the slope required by equation (2). For a singular strategy to be convergence stable, the trade-off function must be more concave (in the sense of a smaller positive or larger negative second derivative) than the critical function at the point of tangent (de Mazancourt and Dieckmann, 2004). The critical functions thus provide a quick and visual way to judge which trade-off functions imply evolution to a convergence stable singularity. Evolutionary stability of the singular strategy has to be evaluated separately.

Both evolutionary stability and convergence stability of a singular strategy $(x^*, f(x^*))$ depend on the second derivatives

$$E = \left.\frac{\partial^2 s}{\partial y^2}\right|_{y=x=x^*} = [\tilde{s}_{11} + 2\tilde{s}_{12} f'(x^*) + \tilde{s}_{22} f'(x^*)^2] + \tilde{s}_2 f''(x^*) \tag{4}$$

and

$$M = \left.\frac{\partial^2 s}{\partial y \partial x}\right|_{y=x=x^*} = \tilde{s}_{13} + (\tilde{s}_{14} + \tilde{s}_{23}) f'(x^*) + \tilde{s}_{24} f'(x^*)^2 \tag{5}$$

where all derivatives of $\tilde{s}$ are evaluated at $(x^*, f(x^*), x^*, f(x^*))$. Note that M does not depend on the convexity of the trade-off, $f''(x^*)$. Therefore, by changing only the convexity of the trade-off at the singular strategy (and leaving $x^*, f(x^*)$, and $f'(x^*)$ unchanged), one can change the value of E independently of M.

$(x^*, f(x^*))$ is evolutionarily stable if E is negative, which can be achieved for any $x^*, f(x^*)$, and $f'(x^*)$ if the last term of E, $\tilde{s}_2 f''(x^*)$, is sufficiently small (or large negative). Because $\tilde{s}_2 > 0$, this means that the singular strategy is evolutionarily stable if the trade-off function is locally sufficiently concave. For convergence stability, $E + M$ must be negative. This condition, too, is satisfied if the trade-off is concave enough.

Note the emerging bifurcation pattern (Bowers *et al.*, 2005): If M is negative, then increasing $f''(x^*)$ first causes the loss of evolutionary stability (when E becomes positive) and then the loss of convergence stability (when $E + M$ becomes positive). In the middle range of $f''(x^*)$, where the singular strategy is convergence stable but not evolutionarily stable, the model exhibits evolutionary branching. If M is positive, then the loss of convergence stability precedes the loss of evolutionary stability, and evolutionary branching is not possible.

The sign of M determines whether there are pairs of similar strategies in the vicinity of the singular strategy such that the two strategies can mutually invade and co-exist with one another: Mutual invasibility is possible if M is negative (Geritz *et al.*, 1998). Assume now that a certain point $(x, f(x))$ is singular. This sets the value of $f'(x)$ according to equation (2) and, because M is independent of $f''(x)$ and higher derivatives, fully determines the value of M in equation (5). Each point $(x, f(x))$ can thus be characterized by whether or not mutual invasibility of similar strategies in its neighbourhood is possible when $(x, f(x))$ is singular, and this characterization does not depend on the shape of the trade-off function. As Bowers *et al.* (2005) point out, if a singular strategy admits mutual invasibility in its neighbourhood, then making the trade-off function increasingly convex at the singularity (while keeping its value and slope constant) will turn a convergence stable ESS first into an evolutionary branching point and then into an evolutionary repellor. If mutual invasibility

is not admitted, then increasing the convexity of the trade-off function turns a convergence stable ESS into a repellor ESS ('garden of Eden') and then into an invasible repellor. With a suitably chosen trade-off function, evolutionary branching is therefore possible if and only if there is mutual invasibility ($M < 0$).

CO-EVOLUTION OF TWO SPECIES

For the sake of generality, first I consider the co-evolution of two unrelated species (such as a predator and its prey). The resulting formulas can easily be simplified for dimorphisms of closely related strategies arising via evolutionary branching, where the two strategies differ only in their trait values but share the same trade-off and fitness functions (see below).

Let $(x_1, f(x_1))$ and $(x_2, g(x_2))$ denote the resident strategy of species 1 and of species 2 respectively, where $f(x_1)$ and $g(x_2)$ are the species-specific trade-off functions. The invasion fitness of a mutant y_1 of species 1 can be written as

$$s(y_1; x_1, x_2) = \tilde{s}(y_1, f(y_1), x_1, f(x_1), x_2, g(x_2)) \tag{6a}$$

and, analogously, the invasion fitness of a mutant of species 2 is

$$r(y_2; x_1, x_2) = \tilde{r}(y_2, g(y_2), x_1, f(x_1), x_2, g(x_2)) \tag{6b}$$

assuming again, without loss of generality, that $\tilde{s}_2 > 0$ and $\tilde{r}_2 > 0$.

At an evolutionarily singular species pair, both fitness gradients $[\partial s/\partial y_1]_{y_1 = x_1}$ and $[\partial r/\partial y_2]_{y_2 = x_2}$ vanish, and therefore the slopes of the trade-off functions are, similarly to equation (2),

$$\begin{aligned} f'(x_1^*) &= -\tilde{s}_1/\tilde{s}_2 \\ g'(x_2^*) &= -\tilde{r}_1/\tilde{r}_2 \end{aligned} \tag{7}$$

Here and below, the derivatives of $\tilde{s}$ are evaluated at $(x_1^*, f(x_1^*), x_1^*, f(x_1^*), x_2^*, g(x_2^*))$ and the derivatives of $\tilde{r}$ are evaluated at $(x_2^*, g(x_2^*), x_1^*, f(x_1^*), x_2^*, g(x_2^*))$.

Because the slope $f'(x_1)$ required by equations (7) depends not only on x_1 but also on x_2 (and vice versa), these equations cannot be used to construct a critical function that captures all potential singularities analogously to the monomorphic case. One can, however, use equations (7) to obtain pieces of $f(x_1)$ and $g(x_2)$ near x_1^* and x_2^*, respectively, that make a given species pair $(x_1^*, f(x_1^*))$ and $(x_2^*, g(x_2^*))$ singular.

The singular species pair is locally evolutionarily stable if it cannot be invaded by mutants in either species, i.e. if

$$\begin{aligned} E_1 = \left.\frac{\partial^2 s(y_1, x_1^*, x_2^*)}{\partial y_1^2}\right|_{y_1 = x_1^*} &= [\tilde{s}_{11} + 2\tilde{s}_{12} f'(x_1^*) + \tilde{s}_{22} f'(x_1^*)^2] + \tilde{s}_2 f''(x_1^*) \\ &=: C_1 + \tilde{s}_2 f''(x_1^*) \end{aligned} \tag{8a}$$

and

$$\begin{aligned} E_2 = \left.\frac{\partial^2 r(y_2, x_1^*, x_2^*)}{\partial y_2^2}\right|_{y_2 = x_2^*} &= [\tilde{r}_{11} + 2\tilde{r}_{12} g'(x_2^*) + \tilde{r}_{22} g'(x_2^*)^2] + \tilde{r}_2 g''(x_2^*) \\ &=: C_2 + \tilde{r}_2 g''(x_2^*) \end{aligned} \tag{8b}$$

are negative (Geritz *et al.*, 1998). This condition is a direct generalization of the monomorphic case (cf. equation 4), and will be satisfied if the trade-off functions f and g are sufficiently concave at $(x_1^*, f(x_1^*))$ and at $(x_2^*, g(x_2^*))$, respectively (Rueffler *et al.*, 2004). Hereafter C_1 and C_2 will represent the bracketed terms in equations (8a) and (8b), respectively, which do not contain the second derivatives of the trade-off functions.

The cross-derivatives that characterize mutual invasibility of similar strategies within a species are also straightforward generalizations of the monomorphic case. Two strategies in the vicinity of x_1^* can co-exist within species 1 if

$$M_1 = \left.\frac{\partial^2 s(y_1, x_1, x_2^*)}{\partial y_1 \partial x_1}\right|_{y_1 = x_1 = x_1^*} = \tilde{s}_{13} + (\tilde{s}_{14} + \tilde{s}_{23}) f'(x_1^*) + \tilde{s}_{24} f'(x_1^*)^2 \tag{9a}$$

is negative, whereas mutual invasibility within species 2 is possible if

$$M_2 = \left.\frac{\partial^2 r(y_2, x_1^*, x_2)}{\partial y_2 \partial x_2}\right|_{y_2 = x_2 = x_2^*} = \tilde{r}_{15} + (\tilde{r}_{16} + \tilde{r}_{25}) g'(x_2^*) + \tilde{r}_{26} g'(x_2^*)^2 \tag{9b}$$

is negative. As in the monomorphic case, M_1 and M_2 do not depend on the second derivatives of the trade-off functions.

Convergence stability in two dimensions is a more difficult problem. If one could prevent evolution in species 2 and thus keep $x_2 = x_2^*$ constant, then, by the direct generalization of the monomorphic case, x_1 would evolve to x_1^* from its neighbourhood if

$$E_1 + M_1 = \tilde{s}_2 f''(x_1^*) + C_1 + M_1 < 0 \tag{10a}$$

whereas in the reverse case, x_2 would evolve to x_2^* if

$$E_2 + M_2 = \tilde{r}_2 g''(x_2^*) + C_2 + M_2 < 0 \tag{10b}$$

These conditions are referred to as 'isoclinic stability'. Isoclinic stability of both x_1^* and x_2^* is, however, neither necessary nor sufficient to ensure convergence stability when both species evolve (Marrow *et al.*, 1996; Matessi and Di Pasquale, 1996). Moreover, convergence stability may be affected by the relative speed of evolution in the two species (Dieckmann and Law, 1996; Marrow *et al.*, 1996; Leimar, in press).

It can nevertheless be shown that by choosing the trade-off functions f and g sufficiently concave at x_1^* and at x_2^*, respectively, the singularity can be made convergence stable. To do this, I use the results of Matessi and Di Pasquale (1996). They considered two traits that mutate independently such that each individual mutation affects only one or the other trait. Although they had two different traits of the same organism in mind, their results apply equally to the case where two traits evolve in two separate species or the same trait evolves in two co-existing strategies. Matessi and Di Pasquale (1996) envisage the evolutionary trajectory as consisting of many small (but finite) steps that correspond to successive substitutions by invading mutants, and they construct the *most extreme path* in the neighbourhood of (x_1^*, x_2^*), i.e. the trajectory that brings the system as far away from (x_1^*, x_2^*) as possible. If the most extreme path is forced to converge to (x_1^*, x_2^*), then no trajectory can diverge and the singularity is necessarily convergence stable. Note that the most extreme path may be such that many consecutive steps are taken such that only species 1 mutates, and then many other steps are taken such that only species 2 mutates. Obviously, such trajectories are highly improbable; real trajectories may converge even if the most

extreme path does not. Convergence of the most extreme path has therefore been termed *absolute convergence* (Leimar, 2001).

Two conditions must be met for absolute convergence stability of (x_1^*, x_2^*) (Matessi and Di Pasquale, 1996). First, both x_1^* and x_2^* must have isoclinic stability (inequalities 10a, b); second, the inequality

$$\left(\frac{\partial^2 s}{\partial y_1^2}+\frac{\partial^2 s}{\partial x_1 \partial y_1}\right)\left(\frac{\partial^2 r}{\partial y_2^2}+\frac{\partial^2 r}{\partial x_2 \partial y_2}\right)>\left|\frac{\partial^2 s}{\partial x_2 \partial y_1}\,\frac{\partial^2 r}{\partial x_1 \partial y_2}\right| \tag{11}$$

must hold at the singularity.

Since isoclinic stability is the direct formal generalization of monomorphic convergence stability, isoclinic stability must hold if the trade-offs are sufficiently concave respectively at x_1^* and at x_2^*. Indeed, it is obvious from (10a, b) that isoclinic stability holds for x_1 whenever $f''(x_1^*) < -(C_1 + M_1)/\tilde{s}_2$ and for x_2 whenever $g''(x_2^*) < -(C_2 + M_2)/\tilde{r}_2$ (recall that $\tilde{s}_2$ and $\tilde{r}_2$ are positive and C_i and M_i contain only the first derivatives of the trade-off functions). For fitness functions in the form of equations (6), the second condition for absolute convergence stability in (11) can be written as

$$(\tilde{s}_2 f''(x_1^*) + C_1 + M_1)\,(\tilde{r}_2 g''(x_2^*) + C_2 + M_2) > |A_1 A_2| \tag{12}$$

where the left-hand side is positive by (10a, b) and

$$A_1 = \left.\frac{\partial^2 s}{\partial x_2 \partial y_1}\right|_{x_1^*, x_2^*} = \tilde{s}_{15} + \tilde{s}_{25} f'(x_1^*) + \tilde{s}_{16} g'(x_2^*) + \tilde{s}_{26} f'(x_1^*)\, g'(x_2^*) \tag{13a}$$

and

$$A_2 = \left.\frac{\partial^2 r}{\partial x_1 \partial y_2}\right|_{x_1^*, x_2^*} = \tilde{r}_{13} + \tilde{r}_{14} f'(x_1^*) + \tilde{r}_{23} g'(x_2^*) + \tilde{r}_{24} f'(x_1^*)\, g'(x_2^*) \tag{13b}$$

do not contain the second derivatives f'' and g''.

The second condition for absolute convergence stability given by (12) holds if the trade-off functions are sufficiently concave, but this implies a stricter condition than only isoclinic stability. The values of $f''(x_1^*)$ and $g''(x_2^*)$ that satisfy (12) lie below an equilateral hyperbola, the asymptotes of which correspond to the isoclinic stability conditions in (10a, b) (Fig. 1). Absolute convergence stability can be ensured for any value of $f''(x_1^*)$ below the bound imposed by isoclinic stability, provided that g is chosen sufficiently concave at x_2^* (and vice versa). In other words, convexity of one trade-off, within the limits of isoclinic stability, can be 'bought' at the cost of convexity of the other trade-off.

If either $A_1 = 0$ or $A_2 = 0$, then isoclinic stability is sufficient to ensure absolute convergence stability. For a geometric interpretation of this case, recall that the co-evolution of two species (or strategies) is often depicted with the help of the x_1- and x_2-isoclines, lines in the phase plane (x_1, x_2) on which the fitness gradient vanishes in the first and in the second species, respectively (Matessi and Di Pasquale, 1996; for a simple example, see Figure 6 of Geritz *et al.*, 1998). The slope of the x_1-isocline at the singularity is $-(E_1 + M_1)/A_1$, whereas the slope of the x_2-isocline is $-A_2/(E_2 + M_2)$. Thus $A_1 = 0$ means that the x_1-isocline is locally parallel to the x_2-axis; similarly, $A_2 = 0$ implies that the x_2-isocline is locally parallel to the x_1-axis. If, at the singularity, the fitness gradient of at least one species is only weakly dependent on the other species' trait value such that A_i is close to zero and, at the same time, isoclinic stability is not too weak, then the x_i-isocline is approximately parallel to the axis. In this case,

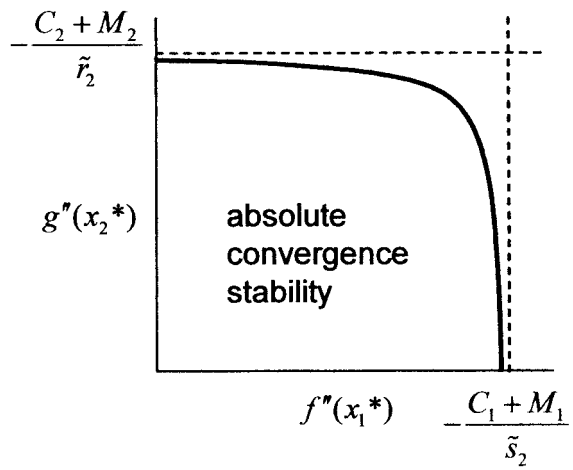

Fig. 1. Absolute convergence stability holds if, at the singular trait values x_1^* and x_2^*, the second derivatives of the trade-off functions are below an equilateral hyperbola with asymptotes $f'' = -(C_1 + M_1)/\tilde{s}_2$ and $g'' = -(C_2 + M_2)/\tilde{r}_2$ (dashed lines). For smaller values of $|A_1A_2|$, the hyperbola is more pressed against its asymptotes.

isoclinic stability of both species guarantees convergence to the singularity. Evolutionary singularities with weak interspecific dependence and nearly horizontal/vertical isoclines appear in several applications (e.g. Geritz *et al.*, 1999; Geritz and Kisdi, 2000).

As in the monomorphic case, M_1 and M_2 play a decisive role in the bifurcation pattern of singular species pairs. Once the singular species pair $(x_1^*, f(x_1^*))$ and $(x_2^*, g(x_2^*))$ is specified, the slopes $f'(x_1^*)$ and $g'(x_2^*)$ are given by equations (7) and C_i, M_i, and A_i are simply numbers. As seen from equations (8), (10), and (12), the singular species pair is both evolutionarily stable and absolutely convergence stable provided that both f and g are locally sufficiently concave. If M_1 is negative, then making f locally more convex leads first to the loss of evolutionary stability and then to the loss of isoclinic stability of x_1^*. As long as x_1^* is isoclinically stable, the singularity has absolute convergence stability provided that $g''(x_2^*)$ is sufficiently negative. It follows that there exist trade-off functions such that species 1 has an evolutionary branching point. If, however, M_1 is positive, then loss of evolutionary and isoclinic stability occurs in the reverse order and absolute convergence stability is necessarily lost before selection turns from stabilizing to disruptive in species 1.

In many simple models, M_i has the same sign for every strategy pair. If M_i is always positive, then evolutionary branching in species i is impossible regardless of the choice of the trade-off functions. If, however, a species pair exists for which M_i is negative, then one can use equations (7)–(10) and (12) to construct trade-off functions such that species i undergoes evolutionary branching. To do this, first choose the trade-off function of species i such that the condition for its isoclinic stability is satisfied but evolutionary stability is not; then choose the trade-off function of the other species concave enough to ensure absolute convergence stability (see an example below).

When following the above recipe, it is sometimes possible to choose the trade-off function of the second species in such a way that not only the first but also the second species has an evolutionary branching point. Note, however, that simultaneous branching points do not

guarantee that both species will indeed split into two distinct strategies: It means only that either of the two species would branch provided that the other species stays at the singularity. If, however, one species branches faster than the other, then this may change the selective environment for the second species such that disruptive selection is lost and the incipient branches of the second species collapse back to monomorphism. An example of such 'missed branching' is given in Kisdi (1999).

It must be noted that absolute convergence stability or isoclinic stability is not necessary for actual convergence given certain frequencies and distributions of mutations (Dieckmann and Law, 1996; Matessi and Di Pasquale, 1996). Evolutionary branching may thus occur also outside the parameter range of absolute convergence stability. Convergence to a singularity that lacks evolutionary stability does not guarantee evolutionary branching when two or more strategies (species) co-evolve: In more than one dimension, mutual invasibility near the singularity (i.e. $M_i < 0$) is a separate requirement for branching (Geritz *et al.*, 1998). If, however, the singularity has *absolute* convergence stability, which implies isoclinic stability ($E_i + M_i < 0$), then lack of evolutionary stability ($E_i > 0$) may occur only with mutual invasibility ($M_i < 0$). In short, absolute convergence stability of a species pair and lack of evolutionary stability in species i guarantee that this species has an evolutionary branching point at the singularity.

EVOLUTION IN DIMORPHIC POPULATIONS

The above results are easily modified to examine the co-evolution of two co-existing strategies that differ in their trait values but share the same trade-off function ($g(x) = f(x)$) and the same fitness function ($\tilde{r} = \tilde{s}$). Such closely related strategies may emerge, for example, as a result of evolutionary branching of a single species.

When substituting $\tilde{s}$ in place of $\tilde{r}$ in the above formulas, care should be taken that the derivatives of $\tilde{s}$ will be evaluated at two different points. To simplify notation, below I shall use superscripts as in $\tilde{s}_2^{(i)}$ to denote the value of $\tilde{s}_2$ at the point $(x_i^*, f(x_i^*), x_1^*, f(x_1^*), x_2^*, f(x_2^*))$, where i can be 1 or 2.

If the dimorphism of $(x_1^*, f(x_1^*))$ and $(x_2^*, f(x_2^*))$ is to be singular, the slope of the trade-off function at x_1^* and x_2^* must be

$$f'(x_1^*) = -\tilde{s}_1^{(1)}/\tilde{s}_2^{(1)}$$
$$f'(x_2^*) = -\tilde{s}_1^{(2)}/\tilde{s}_2^{(2)} \tag{14}$$

Because one evolutionarily singular dimorphism requires specific slopes of the same trade-off function at two distinct points, a full critical function analogous to the monomorphic case cannot be constructed. One can nevertheless obtain two pieces of $f(x)$ in the vicinity of x_1^* and x_2^*, respectively, that make the dimorphism singular. For different evolutionary scenarios, these pieces must be sufficiently concave or convex. To construct concrete examples for these scenarios, one can incorporate the two pieces determined by the local conditions at x_1^* and x_2^* into a full, biologically reasonable trade-off function (see Geritz *et al.*, submitted, for an example).

The expressions for E_i, C_i, M_i, and A_i are easily obtained from the two-species formulas and are listed for convenience in the Appendix. The conclusions of the previous section remain valid. Specifically, the dimorphism is evolutionarily stable as well as absolutely convergence stable if the trade-off function is sufficiently concave at both x_1^* and x_2^*.

Evolutionary branching of strategy i is possible with some trade-off functions if and only if M_i is negative.

AN EXAMPLE

To illustrate the results in a two-species system, consider a predator–prey model where both the prey and the predator evolve the fraction of time they are active (x_1 and x_2, respectively). More active prey have a higher birth rate, but while active, prey suffer from predation. More active predators can catch more prey and hence produce more offspring, but they, too, are vulnerable when active and therefore have a higher death rate. Both prey and predator have intraspecific density dependence in their death rates. The population dynamics of prey (N) and predator (P) follow

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= N(f(x_1) - hN - cx_1x_2P) \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= P(ecx_1x_2N - kP - 1/g(x_2)) \end{aligned} \tag{15}$$

where x_1N and x_2P are the numbers of active prey and predator, respectively, c is the capture rate, e is the conversion efficiency of the predator, h and k are positive constants characterizing the strength of intraspecific density dependence, and $f(x_1)$ is the birth rate of a prey that is active for fraction x_1 of its time. To keep the convention that $\tilde{r}_2$ is positive, I define $g(x_2)$ to be the expected life span of a predator individual with activity x_2; the death rate is then $1/g(x_2)$. For the predator to be viable, $ecx_1x_2f(x_1)g(x_2) - h$ must be positive. There is a single non-trivial equilibrium of the population dynamics, which is stable whenever the predator is viable. A similar model, but with only the prey evolving, has been investigated by Bowers *et al.* (2003).

In this model, the invasion fitness of a rare mutant prey with strategy y_1 is $\tilde{s} = f(y_1) - h\hat{N} - cy_1x_2\hat{P}$, whereas the invasion fitness of a mutant predator y_2 is $\tilde{r} = ecx_1y_2\hat{N} - k\hat{P} - 1/g(y_2)$, where $\hat{N}$ and $\hat{P}$ are the equilibrium densities of prey and predator, respectively, from equations (15); note that both $\hat{N}$ and $\hat{P}$ depend on $x_1, f(x_1)$, x_2, and $g(x_2)$.

The species pair $(x_1, f(x_1))$ and $(x_2, g(x_2))$ is singular if the slopes of the trade-off functions are

$$f'(x_1) = -\frac{cx_2(h - ecx_1x_2f(x_1)g(x_2))}{g(x_2)(hk + ec^2x_1^2x_2^2)}$$

and

$$g'(x_2) = -\frac{ecx_1g(x_2)(cx_1x_2 + kf(x_1)g(x_2))}{hk + ec^2x_1^2x_2^2}$$

respectively (as only singular trait values need to be considered, I omit the stars for readability). Using these slopes, the quantities M_1 and M_2 evaluate to

$$M_1 = -\frac{ec^2hx_2^2(cx_1x_2 + kf(x_1)g(x_2))}{g(x_2)(hk + ec^2x_1^2x_2^2)^2} \tag{16a}$$

and

$$M_2 = -\frac{ec^2kx_1^2(ecx_1x_2f(x_1)g(x_2) - h)}{g(x_2)(hk + ec^2x_1^2x_2^2)^2} \tag{16b}$$

Both M_1 and M_2 are negative whenever the predator is viable. This means that mutual invasibility is possible in both species near any singularity, and trade-off functions exist such that evolutionary branching occurs in the prey or in the predator.

The prey strategy is evolutionarily stable if and only if its trade-off is concave, since

$$E_1 = f''(x_1) \tag{17a}$$

For the predator to be evolutionarily stable, its trade-off may also be somewhat convex as long as

$$E_2 = -\frac{2}{g(x_2)}\left(\frac{ecx_1(cx_1x_2 + kf(x_1)g(x_2))}{hk + ec^2x_1^2x_2^2}\right)^2 + \frac{g''(x_2)}{g(x_2)^2} \tag{17b}$$

is negative. Absolute convergence stability also depends on the cross-derivatives A_1 and A_2; in this model, they evaluate to $A_1 = hM_2/ecx_1^2$ and $A_2 = -kM_1/cx_2^2$.

I use this model to illustrate how one can construct examples for evolution to an ESS species pair and for evolutionary branching. I fix the parameter values at $h = 1$, $k = 0.4$, $c = 10$, and $e = 0.05$, and choose the species pair $(x_1^*, f(x_1^*)) = (0.5,\ 2)$ and $(x_2^*,\ g(x_2^*)) = (0.8,\ 4)$ to be singular. Then the slopes of the trade-off functions must be $f'(x_1^*) = 1$ and $g'(x_2^*) = -6$: these derivatives give the first-order terms in a local approximation of the trade-off functions around $(x_1^*, f(x_1^*))$ and $(x_2^*,\ g(x_2^*))$, respectively. To ensure absolute convergence stability, the trade-off functions must be concave enough to satisfy conditions (10a, b) and (12). The thresholds of $f''(x_1^*)$ and $g''(x_2^*)$ can easily be computed using M_1, M_2, E_1, and E_2 calculated above. The results are shown in Fig. 2 together with the conditions for evolutionary stability from (17a, b). From Fig. 2, one can choose the second derivatives of the trade-off functions to obtain various evolutionary outcomes. The second-order local approximations of the trade-off functions can be extended arbitrarily over the full range of the trait values.

An evolutionarily stable species pair that has absolute convergence stability is always possible and will result for small (or large negative) values of $f''(x_1^*)$ and $g''(x_2^*)$ (area 1 in Fig. 2). Because both M_1 and M_2 are negative in this model, it is also possible to choose $f''(x_1^*)$ and $g''(x_2^*)$ such that the prey undergoes evolutionary branching (area 2) or such that the predator undergoes branching (area 3). With the parameters chosen here, the two species can also have branching points simultaneously within the region of absolute convergence stability in Fig. 2 (area 4). For some other parameter values, however, this is not the case. The straight lines delineating evolutionary stability may cross above the hyperbola, in which case a singularity with absolute convergence stability cannot be a branching point for both species. Recall the caveats that a simultaneous branching point does not ensure that both species do branch (Kisdi, 1999), and that absolute convergence stability is only a sufficient but not a necessary condition, and therefore evolutionary branching (or, with other parameter values, evolution to an ESS species pair) may occur also outside the region of absolute convergence stability.

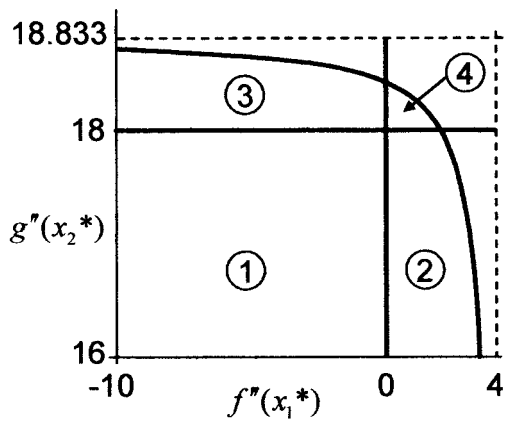

Fig. 2. Stability properties of the singular species pair $(x_1^*, f(x_1^*)) = (0.5, 2)$ and $(x_2^*, g(x_2^*)) = (0.8, 4)$ in the predator–prey model with parameters $h = 1$, $k = 0.4$, $c = 10$, and $e = 0.05$. The conditions for absolute convergence stability in (10a, b) and (12) evaluate to $f''(x_1^*) < 4$, $g''(x_2^*) < 18.833$ (dashed lines), and $(f''(x_1^*) - 4)(g''(x_2^*) - 18.833) > 1.667$ (hyperbola), respectively. The evolutionary stability conditions (17a, b) are $f''(x_1^*) < 0$ and $g''(x_2^*) < 18$ (straight lines). If the convexity of the trade-off functions are chosen from area 1, both prey and predator are evolutionarily stable; in area 2, the prey undergoes evolutionary branching; in area 3, the predator undergoes branching. In area 4, both species have an evolutionary branching point and at least one of them will branch (see text).

DISCUSSION

In simple models, the shape of the trade-off may be left unspecified; predictions are then derived depending on the shape (particularly the convexity) of the trade-off. For example, Levins' fitness set approach predicts the evolution of a single generalist when the trade-off between fitness in two habitats is concave and the evolution of specialists when the trade-off is convex (Levins, 1962). Results of this type are valuable as they are mathematically complete, they specify the biological conditions leading to various evolutionary outcomes, and they offer insight into the underlying selection mechanisms. Moreover, if such a simple model is adequate for the experimental system at hand, one can even infer the shape of the trade-off from the observed evolutionary outcome (Mealor and Boots, 2006).

In more complex models and particularly when a model is amenable only to numerical analysis, the standard practice has been to assume trade-off functions *ad hoc*, thereby losing the advantages of general unspecified trade-offs. The method of critical function analysis (de Mazancourt and Dieckmann, 2004; Bowers *et al.*, 2005) made it possible to analyse the evolution of monomorphic populations of a single species without *a priori* assuming a certain trade-off function. In this study, I have extended the most important results to two co-evolving species or strategies. Although a full critical function cannot be constructed for two-dimensional problems, one can always ensure absolute convergence stability and evolutionary stability of a singular species pair by choosing their trade-off functions locally sufficiently concave. The critical values of the second derivatives of the trade-off functions can be obtained numerically in arbitrarily complex models.

Bowers *et al.* (2005) noted that by changing the shape of the trade-off function in a single-species model, evolutionary branching can always be achieved whenever mutual invasibility is possible in the neighbourhood of the singular strategy. Mutual invasibility is

characterized by the negative sign of the cross-derivative M, which is independent of the convexity of the trade-off. This result also extends to two-species models in the following way: If M_i is positive, then two similar strategies of species i cannot co-exist and therefore this species cannot undergo branching even if it is under disruptive selection (Geritz *et al.*, 1998). If M_i is negative at a certain species pair, then one can find trade-off functions such that this species pair is singular and species i has an evolutionary branching point. If the trade-off function of the other species is chosen sufficiently concave, then species i branches; if, however, both species have branching points, then it may happen that only one of them branches (Kisdi, 1999).

Critical function analysis and its present extension assume that the shape of the trade-off is unknown and thus we wish to vary it, just as one varies the values of unknown parameters of a model to explore all possible outcomes. This is not the case when two traits are linked via a stoichiometric relationship. For example, the fraction of dormant seeds is one minus the fraction of germinating seeds, which forces a simple linear trade-off between the number of dormant and germinating seeds. Stochastic environments with density dependence impose frequency-dependent selection such that two germination strategies may mutually invade one another, but evolutionary branching of the germination fraction is excluded (Ellner, 1985). In this case, M is negative at the singular germination fraction, but for evolutionary branching the trade-off function should be convex, which is here excluded by the biological interpretation of the model. The model of Olivieri *et al.* (1995) for the evolution of dispersal is a similar case: although mutual invasibility is possible, the authors find that the singular strategy is always an ESS. Here the crucial assumption seems to be that dispersal entails a constant mortality cost (for example, a certain fraction of dispersed seeds land outside the suitable habitat). This leads to a linear trade-off between dispersal and the number of surviving offspring. Presumably, a non-linear cost function could lead to evolutionary branching of dispersal strategies. Such a cost function could result from a trade-off between offspring number and the resources invested in dispersal structures, if dispersal is a non-linear function of the latter.

In many cases, measured trade-offs depend on the environmental conditions and thus change in time; in contrast, critical function analysis assumes them to be constant. To circumvent this problem, it is often possible to reformulate the model such that the trade-off links two genetically determined traits instead of derived traits that are also influenced by the environment. To take a simplified example, there may be a trade-off between offspring number and offspring survival in bad years, when only the large (strong) offspring survive, but the same trade-off may be weak or non-existent in good years, when virtually all offspring survive. In this case, one could formulate the trade-off between offspring number and offspring size instead of offspring number and survival. Then the environment-dependent relationship between offspring size and survival affects only the formulation of the fitness function (equation 1), which may be arbitrarily complex in the above analysis, but not the trade-off function ($f(x)$) between the number and size of offspring.

As a worked example, I presented a simple predator–prey model to show how the critical function analysis can be extended to two species. This example may be misleading: critical function analysis is something of an overkill to analyse simple models. The example could have been analysed in the traditional way, assuming that $f(x)$ and $g(x)$ are known (without substituting any concrete formula), and writing down the conditions for convergence and evolutionary stability of the singular species pair. If one has to resort to numerical analysis, however, then usually one would first locate the singular strategies numerically and

then investigate their stability properties. In the first step of the numerical procedure, it is necessary to assume some concrete trade-off function to evaluate the fitness gradient and find its zeros. This is where critical function analysis, and its present extension, becomes really helpful: every step of the critical function analysis can be carried out numerically and without specifying the trade-off function. It is beyond the scope of this paper to analyse a complex model numerically, but such an example can be found in Geritz *et al.* (submitted).

ACKNOWLEDGEMENTS

This work was supported financially by the Finnish Academy of Sciences and by the University of Helsinki.

REFERENCES

Bolnick, D.I. and Doebeli, M. 2003. Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution*, **57**: 2433–2449.

Bowers, R.G., White, A., Boots, M., Geritz, S.A.H. and Kisdi. E. 2003. Evolutionary branching/speciation: contrasting results from systems with explicit or emergent carrying capacities. *Evol. Ecol. Res.*, **5**: 883–891.

Bowers, R.G., Hoyle, A., White, A. and Boots, M. 2005. The geometric theory of adaptive evolution: trade-off and invasion plots. *J. Theor. Biol.*, **233**: 363–377.

de Mazancourt, C. and Dieckmann, U. 2004. Trade-off geometries and frequency-dependent selection. *Am. Nat.*, **164**: 765–778.

Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, **34**: 579–612.

Ellner, S. 1985. ESS germination strategies in randomly varying environments I. Logistic-type models. *Theor. Pop. Biol.*, **28**: 50–79.

Fischer, K., Bot, A.N.M., Brakefield, P.M. and Zwaan, B.J. 2006. Do mothers producing large offspring have to sacrifice fecundity? *J. Evol. Biol.*, **19**: 380–391.

Geritz, S.A.H. and Kisdi, E. 2000. Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proc. R. Soc. Lond. B*, **267**: 1671–1678.

Geritz, S.A.H., Kisdi, E., Meszéna, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Geritz, S.A.H., van der Meijden, E. and Metz, J.A.J. 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Pop. Biol.*, **55**: 324–343.

Geritz, S.A.H., Kisdi, E. and Yan, P. submitted. Evolutionary branching and long-term coexistence of cycling predators: critical function analysis. [Submitted to *Theor. Pop. Biol.*, manuscript under review.]

Kisdi, E. 1999. Evolutionary branching under asymmetric competition. *J. Theor. Biol.*, **197**: 149–162.

Kisdi, E. and Geritz, S.A.H. 1999. Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution*, **53**: 993–1008.

Leimar, O. 2001. Evolutionary change and Darwinian demons. *Selection*, **2**: 65–72.

Leimar, O. in press. Multidimensional convergence stability and the canonical adaptive dynamics. In *Elements of Adaptive Dynamics* (U. Dieckmann and J.A.J. Metz, eds.). Cambridge: Cambridge University Press.

Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *Am. Nat.*, **46**: 361–373.

Levins, R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton University Press.

Marrow, P., Dieckmann, U. and Law, R. 1996. Evolutionary dynamics of predator–prey systems: an ecological perspective. *J. Math. Biol.*, **34**: 556–578.

Matessi, C. and Di Pasquale, C. 1996. Long-term evolution of multilocus traits. *J. Math. Biol.*, **34**: 613–653.

Mealor, M.A. and Boots, M. 2006. An indirect approach to imply trade-off shapes: population level patterns in resistance suggest a decreasingly costly resistance mechanism in a model insect system. *J. Evol. Biol.*, **19**: 326–330.

Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198–202.

Olivieri, I., Michalakis, Y. and Gouyon, P.-H. 1995. Metapopulation genetics and the evolution of dispersal. *Am. Nat.*, **146**: 202–228.

Roff, D.A. 1992. *The Evolution of Life Histories*. New York: Chapman & Hall.

Rueffler, C., van Dooren, T.J.M. and Metz, J.A.J. 2004. Adaptive walks on changing landscapes: Levins' approach extended. *Theor. Pop. Biol.*, **65**: 165–178.

Van Dooren, T.J.M., Durinx, M. and Demon, I. 2004. Sexual dimorphism or evolutionary branching? *Evol. Ecol. Res.*, **6**: 857–871.

APPENDIX

Here I list the expressions for E_i, C_i, M_i, and A_i when the two co-existing strategies differ only in their trait values, i.e. $g(x) = f(x)$ and $\tilde{r} = \tilde{s}$. As in the main text, the upper index (i) denotes the derivative to be evaluated at $(x_i^*, f(x_i^*), x_1^*, f(x_1^*), x_2^*, f(x_2^*))$, where i can be 1 or 2.

A singular dimorphism is evolutionarily stable if

$$E_i = C_i + \tilde{s}_2^{(i)} f''(x_i^*)$$

is negative for $i = 1, 2$, where

$$C_i = \tilde{s}_{11}^{(i)} + 2\tilde{s}_{12}^{(i)} f'(x_i^*) + \tilde{s}_{22}^{(i)} f'(x_i^*)^2$$

Mutual invasibility of resident 1 and its mutant is possible near the singularity if

$$M_1 = \tilde{s}_{13}^{(1)} + (\tilde{s}_{14}^{(1)} + \tilde{s}_{23}^{(1)}) f'(x_1^*) + \tilde{s}_{24}^{(1)} f'(x_1^*)^2$$

is negative; the analogous expression for resident 2 is

$$M_2 = \tilde{s}_{15}^{(2)} + (\tilde{s}_{16}^{(2)} + \tilde{s}_{25}^{(2)}) f'(x_2^*) + \tilde{s}_{26}^{(2)} f'(x_2^*)^2$$

The condition for isoclinic stability of x_i^* remains $E_i + M_i < 0$, and absolute convergence stability also requires $(E_1 + M_1)(E_2 + M_2) > |A_1 A_2|$ with

$$A_1 = \tilde{s}_{15}^{(1)} + \tilde{s}_{25}^{(1)} f'(x_1^*) + \tilde{s}_{16}^{(1)} f'(x_2^*) + \tilde{s}_{26}^{(1)} f'(x_1^*) f'(x_2^*)$$

and

$$A_2 = \tilde{s}_{13}^{(2)} + \tilde{s}_{14}^{(2)} f'(x_1^*) + \tilde{s}_{23}^{(2)} f'(x_2^*) + \tilde{s}_{24}^{(2)} f'(x_1^*) f'(x_2^*)$$