



Adaptive dynamics of Lotka–Volterra systems with trade-offs: the role of interspecific parameter dependence in branching

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Abstract

We determine the adaptive dynamics of a general Lotka–Volterra system containing an intraspecific parameter dependency – in the form of an explicit functional trade-off between evolving parameters – and interspecific parameter dependencies – arising from modelling species interactions. We develop expressions for the fitness of a mutant strategy in a multi-species resident environment, the position of the singular strategy in such systems and the non-mixed second-order partial derivatives of the mutant fitness. These expressions can be used to determine the evolutionary behaviour of the system. The type of behaviour expected depends on the curvature of the trade-off function and can be interpreted in a biologically intuitive manner using the rate of acceleration/deceleration of the costs implicit in the trade-off function. We show that for evolutionary branching to occur we require that one (or both) of the traded-off parameters includes an interspecific parameter dependency and that the trade-off function has weakly accelerating costs. This could have important implications for understanding the type of mechanisms that cause speciation.

The general theory is motivated by using adaptive dynamics to examine evolution in a predator–prey system. The applicability of the general theory as a tool for examining specific systems is highlighted by calculating the evolutionary behaviour in a three species (prey–predator–predator) system.

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1. Introduction

In this paper we investigate the adaptive dynamics of Lotka–Volterra systems when there is an explicit functional trade-off between two evolving parameters and when the system contains other, natural, dependencies between parameters. Parameter trade-offs occur intra-specifically for energetic reasons – a gain in one area of a species’ life history must be balanced by a loss in another. Parameters dependencies occur inter-specifically in a similar way – they express dependence between aspects of the gains or losses experienced by two species due to the biology of their interaction. A good example of a parameter dependency is provided when one considers how an increase in prey susceptibility to predation leads to an increase in the benefit from predation for the predator in predator–prey systems (see (1) and (2)). The consideration of dependent parameters represents the next step of complexity to that considered in [1] in classifying the adaptive dynamics of ecological systems with trade-offs. Including this extra complexity allows for more complicated evolutionary dynamics including the possibility of evolutionary branching, a proposed mechanism for sympatric speciation.

The theory of adaptive dynamics [2–4] assesses the fitness of new types of individuals that arise at low density from small mutations around an established resident strategy. A successful mutant must initially prosper in the environment determined by the resident and if this is the case the mutant’s density will increase and begin to shape the environment. In the long-term the mutant may coexist with the original or oust it to become the new resident itself. The key expression in the analysis of adaptive dynamics is the fitness function of the mutant strategy which is calculated as the per capita growth rate of a mutant strategy, y , in an environment determined by the resident population, x , and denoted $s_x(y)$. If $s_x(y)$ is negative the mutant dies out; if $s_x(y)$ is positive it will spread. Given that mutations are small, the population will evolve in the direction of the local fitness gradient, $[\partial s_x(y)/\partial x]_{y=x}$, until it reaches the neighbourhood of a ‘singular strategy’, x^* , for which the fitness gradient is zero. The behaviour at the singular strategy is determined from combinations of the associated second-order partial derivatives of the fitness function with respect to the mutant and resident strategies and can be characterised by two properties (Table 1). For instance if x^* is not Convergence Stable (CS) and not an Evolutionary Unbeatable Strategy (EUS) it is an evolutionary repellor [2] whereas if it is not CS but is EUS it exhibits what is known as a Garden of Eden evolutionary behaviour [5]. If x^* is CS and EUS then it is an evolutionary attractor [2,4]. The phenomenon of branching occurs when x^* is CS but not EUS. Here we evolve towards x^* but when close by undergo disruptive selection and two distinct strategies coexist either side of x^* . (See [2–4] for more details on the theory of adaptive dynamics.)

Table 1
Properties of the singular strategy, x^* (see [4])

Property	Characteristic
Evolutionarily unbeatable strategy (EUS)	$B < 0$
Convergence stable (CS)	$A - B > 0$

$$A = \frac{\partial^2 s_x(y)}{\partial x^2} \Big|_{y=x=x^*} \quad B = \frac{\partial^2 s_x(y)}{\partial y^2} \Big|_{y=x=x^*}$$

In this study we will consider the evolution of model parameters in Lotka–Volterra systems. Previous studies have examined parameter evolution in specific systems [6–8] but have not focussed on the explicit relationship between parameters and instead link parameters through a relationship with trait values. Explicit functions are required which link each evolving parameter to the traits and the association between parameters is not transparent. Functional trade-offs make clear the connection between parameters and are a subset of the parameterised relationships. The straightforward nature of the connection when using functional trade-offs allows the adaptive behaviour to be classified more generally. As well as providing an advantage mathematically functional trade-offs are also biologically realistic. They arise due to energetic constraints that require that a gain in one area of a species' life history must be balanced by a loss in another and are fundamental in real systems [9,10]. They are represented mathematically by linking parameter pairs using a functional relationship. The study by Bowers and White [1] considered a sub-class of Lotka–Volterra systems in which all the parameters – except those linked by the trade-off – are independent. They showed that these systems could only exhibit evolutionary attractor or repeller dynamics regardless of the number of species which make up the resident environment of the evolving species or the trade-off parameter pair. Branching points (and therefore speciation) were not possible. Studies using more complex specific models that include parameter trade-offs have investigated the evolution of resistance to parasites [11], the evolution of polymorphism in Levene-type models [12] and the role of explicit versus emergent carrying capacities in predator–prey models [13] and have shown that evolutionary branching can occur. The most notable difference between the underlying Lotka–Volterra structure is that the systems in [1] omit interspecific parameter dependencies whereas those of [11–13] include them. The direct biological relevance of trade-offs, the fact that they can be used as a foundation from which to understand the more detailed trait related systems and evidence that different Lotka–Volterra set-ups with trade-offs can exhibit different evolutionary behaviour means that it is important to examine the evolutionary consequences of trade-offs in systems with interspecific parameter dependencies in more detail.

The aim of this paper is to further develop the general theory of adaptive dynamics with trade-offs by extending the class of Lotka–Volterra systems classified by Bowers and White [1] to include models with interspecific parameter dependencies. Any change in the evolutionary behaviour, compared to that possible in [1], can be attributed directly to the added complexity in the model set-up and therefore the increased biological realism. To motivate the general theory we will investigate the adaptive dynamics of a predator–prey system (see Example 1, Eqs. (1) and (2)). We will then apply the methodology used in the predator–prey example to examine the adaptive dynamics of a general Lotka–Volterra system which can contain parameter dependencies. This will provide expressions for the fitness of the evolving species, the position of the singular strategy x^* and the singular values of the non-mixed second-order partial derivatives of fitness with respect to the mutant and resident strategies. This information can be used to provide a classification of the possible evolutionary behaviour in general Lotka–Volterra systems with trade-offs. The expressions can also be used directly to calculate the evolutionary dynamics of specific systems. We illustrate this in Example 2 (Eqs. (36)–(38)) where we determine the evolutionary behaviour of a 3-species (prey–predator–predator) system.

2. Results

2.1. Example 1: predator–prey

Eqs. (1) and (2) represent a multi-strain predator–prey system in which N_i^1 represents the density of the prey strain i when $i \in J1$ (the set of all possible prey strains) and N_i^2 the density of predator strain i when $i \in J2$ (the set of all possible predator strains). The dynamics satisfy

$$\frac{dN_i^1}{dt} = N_i^1 \left(a_i - \sum_{j \in J1} b_{ij} N_j^1 - \sum_{j \in J2} c_{ij} N_j^2 \right) \quad \text{for } i \in J1, \tag{1}$$

$$\frac{dN_i^2}{dt} = N_i^2 \left(d_i - \sum_{j \in J2} e_{ij} N_j^2 + \sum_{j \in J1} c_{ji} g_{ij} N_j^1 \right), \quad \text{for } i \in J2. \tag{2}$$

Here a_i is the intrinsic growth rate of prey strain i , b_{ij} is the rate of competition of prey strain j on prey strain i , c_{ij} is the rate of susceptibility of prey strain i to predation from predator strain j , d_i is the intrinsic growth rate of predator strain i , e_{ij} is the rate of competition of predator strain j on predator strain i (for resources other than prey strains $i \in A1$) and $c_{ji} g_{ij}$ is the rate of benefit to predator strain i of predation on prey strain j . Note here the prey’s susceptibility to predation c_{ij} is the composite of the prey’s ability to ‘avoid’ the predator (which varies with prey strain since strains adopt different strategies) and the predator’s ability to ‘catch’ a particular prey strain (which can be fixed as in (6) below where only consider one predator strain).

For this system we can consider the following cases of species evolution:

- (i) prey evolution with a trade-off between a and c (a trade-off including the intraspecific competition term b is not considered for technical reasons explained in [1]);
- (ii) predator evolution with a trade-off between d and g or between d and c (as above we do not consider trade-offs including the intraspecific competition term e).

In each case we consider the invasion of a mutant strain into an established resident community X which is monomorphic in each species and consists of a prey strain x_1 and a predator strain x_2 (i.e. $X = \{x_1, x_2\}$). We denote mutant prey strains by y_1 and mutant predator strains by y_2 . Since the resident community is in equilibrium we know that the fitness of the resident prey and predator strain denoted $s_X(x_1)$ and $s_X(x_2)$ respectively are zero. Thus the following expressions hold:

$$s_X(x_1) = a_{x_1} - b_{x_1 x_1} N^1 - c_{x_1 x_2} N^2 = 0, \tag{3}$$

$$s_X(x_2) = d_{x_2} - e_{x_2 x_2} N^2 + c_{x_1 x_2} g_{x_2 x_1} N^1 = 0. \tag{4}$$

Here,

$$N^1 = \frac{a_{x_1} e_{x_2 x_2} - c_{x_1 x_2} d_{x_2}}{b_{x_1 x_1} e_{x_2 x_2} + g_{x_2 x_1} (c_{x_1 x_2})^2} \quad \text{and} \quad N^2 = \frac{b_{x_1 x_1} d_{x_2} + c_{x_1 x_2} g_{x_2 x_1} a_{x_1}}{b_{x_1 x_1} e_{x_2 x_2} + g_{x_2 x_1} (c_{x_1 x_2})^2} \tag{5}$$

are the equilibrium densities of the resident strains determined by solving (3) and (4) simultaneously. (Note the subscripts have been dropped from N^1 and N^2 as the superscript is sufficient to distinguish the strain in a resident community monomorphic in each species.) Direct calculation shows that if a coexistence steady state exists (i.e. $N^1 > 0$ and $N^2 > 0$) then it is stable. We consider the cases (i) and (ii) introduced above separately and, in each case, regard all the resident parameters except those linked by the trade-off as fixed or non-evolving. If we first consider the evolution of the prey species with a trade-off $a_i = f(c_{ix_2})$ for $i \in J1$ and $b_{ij} = b_{ii} = b_{ji}$ for $i, j \in J1$. This trade-off reflects the fact that energetic or other constraints will mean that an increase in growth, a , will be bought at the cost of an increased prey susceptibility to predation, c (as here the predator does not evolve, the evolution of c is dependent on the prey only). The fitness function for the mutant prey strain, y_1 is

$$s_X(y_1) = (f(c_{y_1x_2}) - f(c_{x_1x_2})) - (c_{y_1x_2} - c_{x_1x_2})N^2, \tag{6}$$

where we have used (3) and the definition of the trade-off to eliminate the terms in b . For f to be a trade-off function in (6) we recognise that $f' > 0$ (i.e. an increase in growth, a , implies an increase in susceptibility to predation, c). Since we have freedom to choose a 1–1 relationship between prey strains and parameter values we can identify $c_{x_1x_2}$ with $x = x_1$ and $c_{y_1x_2}$ with $y = y_1$. (We can do this because the predator strain x_2 is fixed – it refers to a different non-evolving species.) We can then write (6) as

$$s_X(y) = (f(y) - f(x)) - (y - x)N^2. \tag{7}$$

where we recall that the equilibrium density N^2 depends on x but not y . The population will evolve in the direction of its local fitness gradient [2–4] defined as $\partial s_X(y)/\partial y|_{y=x}$, which from (7) can be expressed as

$$\left. \frac{\partial s_X(y)}{\partial y} \right|_{y=x} = f'(x) - N^2. \tag{8}$$

Hence, from (8), if f is not a trade-off, the fitness gradient has negative sign and evolution continues until the minimum value of the evolving parameter is reached. In the other case – on which we shall concentrate – the fitness gradient may change sign and here evolution may continue until the minimum or maximum value of the evolving parameter is obtained or until it reaches a neighbourhood of a strategy for which the fitness gradient is zero. Such a strategy is known as evolutionarily singular, denoted x^* , and occurs when

$$f'(x^*) = N^2|_*. \tag{9}$$

(We use asterisks generally to denote evaluation at the singular parameter values.) To determine the properties of the singular strategy requires knowledge of the second-order partial derivatives of $s_X(y)$ with respect to mutant and resident strategies at the singular strategy [2–4]. We use (5), (7) and (9) (recalling that x and $c_{x_1x_2}$ have been identified) to show that

$$\left. \frac{\partial^2 s_X(y)}{\partial x^2} \right|_* = -f''(x^*) + 2 \left. \frac{\partial N^2}{\partial x} \right|_* = -f''(x^*) + 2 \frac{bg}{be + g(x^*)^2} N^1|_*, \tag{10}$$

$$\left. \frac{\partial^2 s_X(y)}{\partial y^2} \right|_* = f''(x^*). \tag{11}$$

(We drop subscripts from the non-evolving parameters.) We can classify the behaviour at the singular strategy by considering the curvature of the trade-off function and by using the definitions in Table 1. When $f''(x^*) < 0$ the singular strategy x^* is an EUS, is necessarily CS and is therefore an evolutionary attractor (Fig. 1(a) and (b)). When $f''(x^*) > 0$ then the singular strategy is not EUS. It is CS if

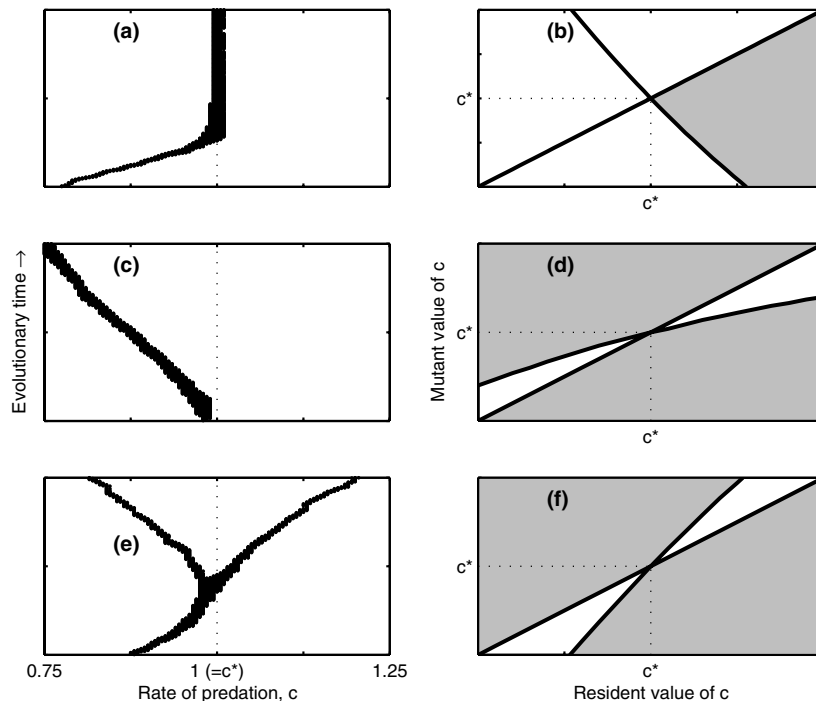


Fig. 1. Simulations of Eqs. (1) and (2) for the evolution of the prey showing how the rate of predation, c , evolves over time and the corresponding pairwise invasibility plots (PIPs) near the singular point showing whether the mutant fitness, $s_X(y)$, is positive (shaded) or negative (unshaded). In the PIPs the diagonal is the line where resident and mutant values of c are equal (i.e. $y = x$). Parameters are $b = 1$, $d = 1$, $e = 1$ and $g = 1$ and the trade-off $a = f(c) = \alpha c^2 + 2c + 3\alpha + 1$ which fixes a singularity $c^* = 1$. In (a) and (b) $\alpha = -0.5$ and therefore $f''(c^*) < 0$ and c^* is an evolutionary attractor, in (c) and (d) $\alpha = 0.75$ and therefore $f''(c^*) > 0$ but Eq. (12) is not satisfied and c^* is an evolutionary repeller and in (e) and (f) $\alpha = 0.25$ and Eq. (12) is satisfied and c^* is an evolutionary branching point. In the simulations the population dynamics were numerically solved for a fixed time (t) according to Eqs. (1) and (2) starting with a monomorphic population. Mutant strategies were generated by small deviations around the current strategies and introduced at low density. Then the population dynamics were solved for a further time t with strategies whose population density fell below a low threshold considered extinct and removed before considering new mutations. In this way the parameter c could evolve. Note the simulations are not mutation-limited (i.e. new mutants could evolve before previous mutants had reached equilibrium or gone extinct) which accounts for thickness of the lines in figures (a), (c) and (e). This however did not confound the model predictions.

Table 2
Properties of the singular strategy for predator evolution in the predator–prey system (1), (2)

	Trade-off	Equivalence	Singular strategy, x^* occurs when	$\left. \frac{\partial^2 s_X(y)}{\partial x^2} \right _*$	$\left. \frac{\partial^2 s_X(y)}{\partial y^2} \right _*$
1	$d_i = f(g_{ix})$	$x = g_{x_2x_1} \ y = g_{y_2x_1}$	$f'(x^*) = -cN^1 _*$	$-f''(x^*)$	$f'''(x^*)$
2	$d_i = f(c_{xi})$	$x = c_{x_1x_2} \ y = c_{x_1y_2}$	$f'(x^*) = -gN^1 _*$	$-f''(x^*) + 2\frac{ge}{be+g(x^*)^2}N^2 _*$	$f'''(x^*)$

Here recall that the asterisk relates to evaluation at the singular strategy. Subscripts are omitted from non-evolving parameters.

$$f''(x^*) < \left. \frac{\partial N^2}{\partial x} \right|_* \quad \text{or equivalently} \quad f''(x^*) < \frac{bg}{be + g(x^*)^2} N^1|_*. \tag{12}$$

Therefore if (12) holds it is a branching point. Here, disruptive selection will lead to dimorphism in the prey species with distinct prey strains (on either side of x^*) coexisting (Fig. 1(e) and (f)). If the inequality (12) is reversed then the singular strategy is not CS and is therefore an evolutionary repeller (Fig. 1(c) and (d)). The results for predator evolution in the model (1), (2) can be determined in a similar manner and are summarised in Table 2.

Considering the trade-off between d and g (row 1, Table 2) in terms of the results outlined in Table 1 we can see that $A = -B$. Hence when $f''(x^*) < 0$, the singularity is an EUS, is necessarily CS and therefore an evolutionary attractor. When $f''(x^*) > 0$ the singularity is not EUS and not CS and is therefore an evolutionary repeller (see [1]).

If we consider the trade-off between d and c (row 2, Table 2) then the results are analogous to those for prey evolution in that if $f''(x^*) < 0$ we expect an evolutionary attractor, whereas if $f''(x^*) > 0$ then the singularity is a branching point if

$$f''(x^*) < \frac{eg}{be + g(x^*)^2} N^2|_*, \tag{13}$$

and an evolutionary repeller if inequality (13) is reversed.

From this example we observe that if the evolving parameters coupled by the trade-off include the dependent parameter (c in the example) then there is a possibility of branching. When the traded-off parameters do not include the dependent parameter (Table 1, row 1) then there is no possibility of branching – a result in accord with our previous work [1]. We now turn our attention to general theory in order to investigate whether these observations are true of all Lotka–Volterra systems like (1), (2).

2.2. General results for Lotka–Volterra systems with trade-offs and parameter dependencies

To understand the evolutionary behaviour of Lotka–Volterra systems more comprehensively we need to adopt a generalised approach. We consider multi-species, multi-strain Lotka–Volterra systems in which the dynamics of strain i , of species α (where $i \in J_\alpha$ the set of all possible strains of species α), can be represented as

$$\frac{dN_i^\alpha}{dt} = N_i^\alpha \left(\sum_{\beta \in S_\alpha} \sum_{j \in J_\beta} \eta^{\alpha\beta} p_{ij}^{\alpha\beta} N_j^\beta \right). \tag{14}$$

Here, N_i^α is the density of strain i of species α (where $\alpha = 1, 2, \dots, n$), $p_{ij}^{\alpha\beta} > 0$ are parameters associated with interactions between distinct strains of either the same or different species (e.g. within and between species competition and predation) and $\eta^{\alpha\beta} = \pm 1$ accounts for whether the interaction between species α and β has a positive or negative effect on the density of species α . (Here, when the parameter, $p_{ij}^{\alpha\beta}$, represents a between species interaction it can vary as a result of the differing strategies adopted by both species α and β in a similar way to that in which the susceptibility to predation could vary with both predator and prey strains in Example 1.) Furthermore, S_α is the set of all species that interact with species α and J_β is the set of all strains of species β . To allow for the representation of intrinsic parameters (e.g. intrinsic birth and death) it is convenient to include a fictitious species ‘0’ with a single strain ‘ x_0 ’ such that

$$\eta^{x_0} = \pm 1, \quad p_{ix_0}^{\alpha 0} = p_i^\alpha > 0 \quad \text{and} \quad N_{x_0}^0 = 1. \tag{15}$$

We also define $p_{x_0x_0}^{00} = 1$ and $p_{x_0i}^{0\alpha} = 0$ otherwise (which is consistent with (25)). This notation is similar to that outlined in [1] (and [2,14]) but has been modified slightly with a view to making it more tractable. The framework of [1] still holds and the set-up is briefly repeated below in the new notation for clarity and to form the basis from which to understand the behaviour under the more complex representation which allows parameter dependencies. The general analysis below parallels the particular analysis in Example 1.

We let X be a resident community containing a single strain of each species (i.e. $X = (x_1, x_2, \dots, x_\alpha, \dots, x_n)$). Now since we assume the resident community is in equilibrium the fitness function for each resident strain is equal to zero. Therefore, the following holds (with the subscripts on the densities dropped since in a monomorphic community the species type (superscript) can be used to identify the strain)

$$s_X(x_\alpha) = \sum_{\beta \in S_\alpha} \eta^{\alpha\beta} p_{x_\alpha x_\beta}^{\alpha\beta} N^\beta = 0 \quad \text{for } \alpha = 1, 2, \dots, n. \tag{16}$$

The n equations in (16) can be solved to find the equilibrium density for each species. We are interested in the evolution of one species against the resident background population. Let us assume that species α evolves, and that the mutant strain in species α is y_α . By defining the fitness for the mutant species and using the result in (16) we can write

$$s_X(y_\alpha) = \sum_{\beta \in S_\alpha} \left(p_{y_\alpha x_\beta}^{\alpha\beta} - p_{x_\alpha x_\beta}^{\alpha\beta} \right) \eta^{\alpha\beta} N^\beta. \tag{17}$$

We now introduce a trade-off between two parameters by assuming they are related by a condition of the form

$$p_{y_\alpha x_\gamma}^{\alpha\gamma} = f \left(p_{y_\alpha x_\beta}^{\alpha\beta} \right). \tag{18}$$

We assume that all other parameters (i.e. those not involved in the parameter trade-off) are the same for both the mutant and resident, so $p_{y_\alpha x_\phi}^{\alpha\phi} = p_{x_\alpha x_\phi}^{\alpha\phi} \quad \forall \phi \in S_\alpha \neq \{\beta, \gamma\}$. Using (18) we can then write (17) as

$$s_X(y_\alpha) = \left(f \left(p_{y_\alpha x_\beta}^{\alpha\beta} \right) - f \left(p_{x_\alpha x_\beta}^{\alpha\beta} \right) \right) \eta^{\alpha\gamma} N^\gamma + \left(p_{y_\alpha x_\beta}^{\alpha\beta} - p_{x_\alpha x_\beta}^{\alpha\beta} \right) \eta^{\alpha\beta} N^\beta. \tag{19}$$

For f to be a trade-off the two terms above must be of opposite signs so $(\eta^{\alpha\gamma}/\eta^{\alpha\beta})f$ must be decreasing which implies that $(\eta^{\alpha\gamma}/\eta^{\alpha\beta})f' < 0$. Using (19) and by identifying the resident parameter $p_{x_\alpha x_\beta}^{\alpha\beta}$

with x and the mutant parameter $p_{yx}^{\alpha\beta}$ with y we can simplify notation and produce the equivalent result to that in [1], namely,

$$s_X(y) = (f(y) - f(x))\eta^{xy}N^\gamma + (y - x)\eta^{\alpha\beta}N^\beta. \tag{20}$$

The singular strategy, x^* , occurs when the fitness gradient is zero, and for this generalised system this occurs when

$$\left. \frac{\partial s_X(y)}{\partial y} \right|_{y=x} = f'(y)\eta^{xy}N^\gamma + \eta^{\alpha\beta}N^\beta = 0 \Rightarrow f'(x^*) = \frac{-\eta^{\alpha\beta}N^\beta}{\eta^{xy}N^\gamma} \Big|_*. \tag{21}$$

The behaviour at the singular strategy can be determined from combinations of the second-order partial derivative of $s_X(y)$ with respect to the resident and mutant parameters evaluated at the singularity. We find

$$\left. \frac{\partial^2 s_X(y)}{\partial x^2} \right|_* = -f''(x^*)\eta^{xy}N^\gamma \Big|_* - 2f'(x^*)\eta^{xy} \left. \frac{\partial N^\gamma}{\partial x} \right|_* - 2\eta^{\alpha\beta} \left. \frac{\partial N^\beta}{\partial x} \right|_*, \tag{22}$$

$$\left. \frac{\partial^2 s_X(y)}{\partial y^2} \right|_* = f''(x^*)\eta^{xy}N^\gamma \Big|_*. \tag{23}$$

In Bowers and White [1] it is proved that the derivatives of densities appearing in (22) are always zero if the model parameters are independent. In terms of Table 1, we have that $A = -B$ and it then follows that an evolutionary attractor or an evolutionary repeller are the only possibilities. We will show below that when the parameters are not independent, the density derivatives in (22) are not necessarily zero and the range of possible evolutionary behaviour is increased. This has important biological consequences.

2.3. The effect of generalised parameter dependencies

An illustration of a parameter dependency was given in the predator–prey example (1), (2) where the benefit of predation for the predator depended on the susceptibility to predation of the prey (through a linear relation on the parameter c). Our aim here is to give a general account of this phenomenon. As in the example, parameter dependency corresponds to two terms (one for each species) which model the effects of a particular interaction between two species. Therefore if a dependency occurs it will do so between parameters $p_{x_\mu x_\nu}^{\mu\nu}$ and $p_{x_\nu x_\mu}^{\nu\mu}$. The expression for the fitness of the resident strains (16) for species μ can be written

$$s_X(x_\mu) = \sum_{\nu \in S_\mu} \eta^{\mu\nu} p_{x_\mu x_\nu}^{\mu\nu} N_{x_\nu}^\nu = 0, \tag{24}$$

and we can use (24) and (18) to determine some general properties of the derivatives of densities in (22). From (15) we know that

$$N^0 = 1 \Rightarrow \frac{\partial N^0}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} = 0. \tag{25}$$

Assuming the trade-off in (18), which links the evolving species α with species β and γ , we differentiate (24) with respect to $p_{x_\alpha x_\beta}^{\alpha\beta}$ thereby generating the following results:

$$\text{for } \mu \neq \alpha, \beta, \gamma \quad \sum_{v \in S_\mu} \eta^{\mu\nu} p_{x_\mu x_\nu}^{\mu\nu} \frac{\partial N^v}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} = 0, \tag{26}$$

$$\text{for } \mu = \alpha \quad \sum_{v \in S_\mu} \eta^{\alpha v} p_{x_\alpha x_\nu}^{\alpha v} \frac{\partial N^v}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} + \left\{ \eta^{\alpha\gamma} f' \left(p_{x_\alpha x_\beta}^{\alpha\beta} \right) N^\gamma + \eta^{\alpha\beta} N^\beta \right\} = 0, \tag{27}$$

$$\text{for } \mu = \beta \quad \sum_{v \in S_\mu} \eta^{\beta v} p_{x_\beta x_\nu}^{\beta v} \frac{\partial N^v}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} + \eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha = 0, \tag{28}$$

$$\text{for } \mu = \gamma \quad \sum_{v \in S_\mu} \eta^{\gamma v} p_{x_\gamma x_\nu}^{\gamma v} \frac{\partial N^v}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} + \eta^{\gamma\alpha} \frac{p_{x_\gamma x_\alpha}^{\gamma\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha = 0. \tag{29}$$

We can use these equations to determine generalised expressions for the derivatives of densities in Eq. (22). Since we are interested in values at the singular point, the expression in braces in (27) vanishes by (21). We then define M as the $(n + 1$ by $n + 1)$ matrix in which the first row is a 1 followed by n 0's (from 25) and which contains the parameters with their signs $(\eta^{\alpha\beta} p_{x_\alpha x_\beta}^{\alpha\beta})$ in subsequent rows. We also let $N = (N^0, N^1, \dots, N^n)^T$ the column vector of species densities. (See Example 2 for a specific description of M and N .) We find from (25)–(29) that

$$M \frac{\partial N}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} = -\eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha e_\beta - \eta^{\gamma\alpha} \frac{\partial p_{x_\gamma x_\alpha}^{\gamma\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha e_\gamma, \tag{30}$$

where e_β and e_γ are base vectors (i.e. e_β has value 1 in the β row position and 0's in all other positions). This implies that

$$\frac{\partial N}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} = -\eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha M^{-1} e_\beta - \eta^{\gamma\alpha} \frac{\partial p_{x_\gamma x_\alpha}^{\gamma\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha M^{-1} e_\gamma. \tag{31}$$

Using (31) we see that the required derivatives in (22) can be written as

$$\begin{aligned} \frac{\partial N^\beta}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} &= -\eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha (M^{-1})_{\beta\beta} - \eta^{\gamma\alpha} \frac{\partial p_{x_\gamma x_\alpha}^{\gamma\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha (M^{-1})_{\beta\gamma} \\ &= -\eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha \frac{\text{cofactor}_{\beta\beta}(M)}{\det M} - \eta^{\gamma\alpha} \frac{\partial p_{x_\gamma x_\alpha}^{\gamma\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha \frac{\text{cofactor}_{\gamma\beta}(M)}{\det M}, \end{aligned} \tag{32}$$

$$\begin{aligned} \frac{\partial N^\gamma}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} &= -\eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha (M^{-1})_{\gamma\beta} - \eta^{\gamma\alpha} \frac{\partial p_{x_\gamma x_\alpha}^{\gamma\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha (M^{-1})_{\gamma\gamma} \\ &= -\eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha \frac{\text{cofactor}_{\beta\gamma}(M)}{\det M} - \eta^{\gamma\alpha} \frac{\partial p_{x_\gamma x_\alpha}^{\gamma\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha \frac{\text{cofactor}_{\gamma\gamma}(M)}{\det M}. \end{aligned} \tag{33}$$

We can then use (32) and (33) in conjunction with (22) and (23) to determine the general behaviour at the singular strategy. We consider some particular cases below.

The analysis of this section can be undertaken in a more general setting where the parameters $p_{ij}^{\alpha\beta}$ in (14) are replaced by parameters $d_{ij}^{\alpha\beta}$ which can be composites of the (underlying) $p_{ij}^{\alpha\beta}$. While this can be useful computationally it is more complicated notationally and so the results are relegated to **Appendix A**.

1. *The trade-off does not involve a dependent parameter.*

If the trade-off does not involve a dependent parameter then both the parameter derivatives ($\partial p_{x\beta x\alpha}^{\beta\alpha} / \partial p_{x\alpha x\beta}^{\alpha\beta}$ and $\partial p_{x\gamma x\alpha}^{\gamma\alpha} / \partial p_{x\alpha x\beta}^{\alpha\beta}$) in (32) and (33) are zero. Thus using (22) and (23) we see that in terms of **Table 1** $A = -B$. This parallels the result for the trade-off between $d_i = f(g_{ix})$ in example 1 in which evolutionary attractor or repeller dynamics are the only possibilities. It also extends the results in [1], since here we show that branching is not possible if the traded-off parameters are independent of the other parameters, whereas [1] assumed all the parameters in the system were independent.

2. *Trade-off between intrinsic and interaction parameters, $p_{y_2 x_0}^{\alpha 0} = f(p_{y_2 x_\beta}^{\alpha\beta})$, where $p_{x_2 x_\beta}^{\alpha\beta}$ and $p_{x_\beta x_\alpha}^{\beta\alpha}$ are dependent parameters.*

With this trade-off we identify the species $\gamma = 0$ and can see directly from (25) that $\partial N^\gamma / \partial p_{x_\alpha x_\beta}^{\alpha\beta} = \partial N^0 / \partial p_{x_\alpha x_\beta}^{\alpha\beta} = 0$. Also, $\partial p_{x_\gamma x_\alpha}^{\gamma\alpha} / \partial p_{x_\alpha x_\beta}^{\alpha\beta} = \partial p_{x_0 x_\alpha}^{\alpha 0} / \partial p_{x_\alpha x_\beta}^{\alpha\beta} = 0$, since by definition $p_{x_0 x_\alpha}^{\alpha 0} = 0$ (representing the fact that an intrinsic parameter cannot be a dependent parameter). Thus, (22) becomes

$$\begin{aligned} \frac{\partial^2 s_X(y)}{\partial x^2} &= -f''(x^*)\eta^{\alpha\gamma}N^\gamma|_* + 2\eta^{\alpha\beta}\eta^{\beta\alpha} \frac{\partial p_{x_\beta x_\alpha}^{\beta\alpha}}{\partial p_{x_\alpha x_\beta}^{\alpha\beta}} N^\alpha|_* \frac{\text{cofactor}_{\beta\beta}(M)}{\det M} \\ &= -f''(x^*)\eta^{\alpha\gamma}N^\gamma|_* + 2TN^\gamma|_*, \end{aligned} \tag{34}$$

which defines the quantity T . We can use (23) and (34) to characterise the possible evolutionary behaviour in terms of $\eta^{\alpha\gamma}$ and the sign and magnitude of $f''(x^*)$, 0 and T (**Table 3**).

3. *Trade-off is between two interaction terms $p_{y_2 x_\gamma}^{\alpha\gamma} = f(p_{y_2 x_\beta}^{\alpha\beta})$ where $p_{x_2 x_\beta}^{\alpha\beta}$ and $p_{x_\beta x_\alpha}^{\beta\alpha}$ are dependent parameters and $p_{x_\alpha x_\gamma}^{\alpha\gamma}$ and $p_{x_\gamma x_\alpha}^{\gamma\alpha}$ are not dependent.*

Here we know that $\partial p_{x_\gamma x_\alpha}^{\gamma\alpha} / \partial p_{x_\alpha x_\beta}^{\alpha\beta} = 0$ and this removes one of the terms from Eqs. (32) and (33). Thus using (21), Eq. (22) can be written as

Table 3
Possible evolutionary behaviour in terms of $f''(x^*)$, $\eta^{\alpha\gamma}$, 0 and T

Condition on $f''(x^*)$, $\eta^{\alpha\gamma}$ and T	Characteristic of x^*	Evolutionary behaviour at x^*
$f''(x^*)\eta^{\alpha\gamma} < \min(T, 0)$	EUS, CS	Attractor
$T < f''(x^*)\eta^{\alpha\gamma} < 0$	EUS, not CS	Garden of Eden
$\max(T, 0) < f''(x^*)\eta^{\alpha\gamma}$	not EUS, not CS	Repeller
$0 < f''(x^*)\eta^{\alpha\gamma} < T$	not EUS, CS	Branching point

$$\begin{aligned} \frac{\partial^2 S_X(y)}{\partial x^2} &= -f''(x^*)\eta^{\alpha\gamma}N^\gamma|_* + 2\eta^{\alpha\beta}\eta^{\beta\alpha} \frac{\partial p_{x\beta x\alpha}^{\beta\alpha}}{\partial p_{x\alpha x\beta}^{\alpha\beta}} \frac{N^\alpha|_*}{\det M} \left(\text{cofactor}_{\beta\beta}(M) - \frac{N^\beta|_*}{N^\gamma|_*} \text{cofactor}_{\beta\gamma}(M) \right) \\ &= -f''(x^*)\eta^{\alpha\gamma}N^\gamma|_* + 2TN^\gamma|_*. \end{aligned} \tag{35}$$

Eq. (35) defines T and then as above the behaviour is classified by Table 3.

4. Trade-off is between two interaction terms $p_{y_\alpha x_\gamma}^{\alpha\gamma} = f(p_{y_\alpha x_\beta}^{\alpha\beta})$ where both trade-off parameters are dependent.

When both trade-off parameter have dependencies it is not possible to simplify the expressions in (32) and (33). The definition of T therefore contains four terms. The behaviour is nevertheless classified by Table 3.

2.4. Example 2: a three species system

The general theory described above can be illustrated and made more tangible by way of an example. We choose a three species system in which there is one prey supporting two predators and in which the predators are in direct competition for other resources. This example is chosen as it is possible to generate all the possible evolutionary outcomes described above through different choices of the trade-off parameters.

The model represents a multi-strain three species system in which N_i^1 represents the density of the prey strain i when $i \in J1$ (the set of all possible prey strains), N_i^2 represents the density of predator 1 strain i when $i \in J2$ and N_i^3 represents the density of predator 2 strain i when $i \in J3$. We choose to use the same notation as in the general theory but with the terms of the general theory explicitly defined. The dynamics are represented by

$$\frac{dN_i^1}{dt} = N_i^1 \left(p_{ix_0}^{10} - \sum_{j \in J1} p_{ij}^{11} N_j^1 - \sum_{j \in J2} p_{ij}^{12} N_j^2 - \sum_{j \in J3} p_{ij}^{13} N_j^3 \right) \quad \text{for } i \in J1, \tag{36}$$

$$\frac{dN_i^2}{dt} = N_i^2 \left(p_{ix_0}^{20} - \sum_{j \in J2} p_{ij}^{22} N_j^2 + \sum_{j \in J1} p_{ij}^{21} N_j^1 - \sum_{j \in J3} p_{ij}^{23} N_j^3 \right) \quad \text{for } i \in J2, \tag{37}$$

$$\frac{dN_i^3}{dt} = N_i^3 \left(p_{ix_0}^{30} - \sum_{j \in J3} p_{ij}^{33} N_j^3 + \sum_{j \in J1} p_{ij}^{31} N_j^1 - \sum_{j \in J2} p_{ij}^{32} N_j^2 \right) \quad \text{for } i \in J3. \tag{38}$$

Thus $p_{ix_0}^{10}$, $p_{ix_0}^{20}$ and $p_{ix_0}^{30}$ are the intrinsic growth rates of strain i and p_{ij}^{11} , p_{ij}^{22} and p_{ij}^{33} represent the intraspecific competition of strain j on strain i for the prey, predator 1 and predator 2 species respectively. The parameter p_{ij}^{12} is the susceptibility to predation of prey strain i from predator 1 strain j with this predation converted into births of predator 1 strain i at rate p_{ij}^{21} . Parameter p_{ij}^{13} is the susceptibility to predation of prey strain i from predator 2 strain j with this predation converted into births of predator 2 strain i at rate p_{ij}^{31} . Finally parameter p_{ij}^{23} is the rate of inter-specific competition of predator 2 strain j on predator 1 strain i with p_{ij}^{32} the corresponding inter-specific competition term of predator 1 on predator 2.

We assume a resident population at equilibrium containing one strain of each species, $X = \{x_1, x_2, x_3\}$. We examine the evolution of predator 1 against this background community and for different trade-off combinations, so as to give corresponding explicit results to those outlined generally above. If we assume that there is a mutant strain, y_2 of predator 1 then we can show that the mutant fitness is

$$s_X(y_2) = (p_{y_2}^2 - p_{x_2}^2) - (p_{y_2x_2}^{22} - p_{x_2x_2}^{22})N^2 + (p_{y_2x_1}^{21} - p_{x_2x_1}^{21})N^1 - (p_{y_2x_3}^{23} - p_{x_2x_3}^{23})N^3. \tag{39}$$

We then consider the trade-offs outlined below, remembering that mutant and resident parameters which are not linked by the trade-off are considered equal for each particular calculation. The matrix of parameters, M and the associated column vector N (as defined for (31)) are defined below. Note subscripts are omitted here (and below) when parameters and densities refer to the resident strains.

$$M = \begin{pmatrix} 1 & 0 & 0 & 0 \\ p^{10} & -p^{11} & -p^{12} & -p^{13} \\ p^{20} & p^{21} & -p^{22} & -p^{23} \\ p^{30} & p^{31} & -p^{32} & -p^{33} \end{pmatrix} \quad N = \begin{pmatrix} N^0 \\ N^1 \\ N^2 \\ N^3 \end{pmatrix}. \tag{40}$$

For different sets of trade-offs we identify the terms in the general formulae with the specific terms in this example.

1. *Trade-off:* $p_{y_2x_0}^{20} = f(p_{y_2x_3}^{23})$

Here the intrinsic parameter cannot be repeated and if we assume there is no dependency between the competition parameter p^{23} and p^{32} then the trade-off does not contain any parameter dependencies. The general theory therefore tells us that evolutionary repeller or attractor behaviour is the only possibility.

2. *Trade-off:* $p_{y_2x_0}^{20} = f(p_{y_2x_1}^{21})$

This trade-off links the intrinsic growth rate of predator 1 with the benefit of predation for predator 1 on the prey. The benefit of predation is often related to the susceptibility of the prey to predation and so a dependency is expected between p^{21} and p^{12} (as in Example 1). To produce explicit results we assume $p^{12} = kp^{21}$ then from (21) and using (32) we know the singular strategy occurs when

$$f'(x^*) = \frac{-\eta^{21}N^1|_*}{\eta^{20}N^0|_*} = -N^1|_*. \tag{41}$$

Using the general theory (see (34)) the second derivatives at x^* are as follows:

$$\begin{aligned} \frac{\partial^2 s_X(y)}{\partial x^2} &= -f''(x^*)\eta^{20}N^0|_* + 2\eta^{21}\eta^{12}\frac{\partial p^{12}}{\partial p^{21}}N^2|_* \frac{\text{cofactor}_{11}(M)}{\det M}, \\ &= -f''(x^*) - 2kN^2|_* \frac{p^{22}p^{33} - p^{23}p^{32}}{\det M} = -f''(x^*) + 2TN^0|_*, \end{aligned} \tag{42}$$

$$\frac{\partial^2 s_X(y)}{\partial y^2} = f''(x^*), \tag{43}$$

where $T > 0$ (since $p^{22}p^{33} - p^{23}p^{32} > 0$ and $\det M < 0$ when the 3-species coexistence equilibrium is feasible and stable). From Table 3 (since $\eta^{\alpha\gamma} = \eta^{20} = 1$) we can see that the singular strategy can be

an attractor if $f''(x^*) < 0$, a repeller if $f''(x^*) > T$ and also an evolutionary branching point if $0 < f''(x^*) < T$.

3. *Trade-off*: $p_{y_2x_3}^{23} = f(p_{y_2x_1}^{21})$

This trade-off links the competition rate between predator 1 and predator 2 with the benefit of predation for predator 1 on the prey. As detailed above we do not invoke a dependency between p^{23} and p^{32} but do invoke one between p^{21} and p^{12} and as above assume $p^{12} = kp^{21}$. The singular strategy occurs when

$$f'(x^*) = \frac{-\eta^{21}N^1|_*}{\eta^{23}N^1|_*} = \frac{N^1|_*}{N^3|_*}. \tag{44}$$

Using the general theory (see (35)) the second derivatives at x^* are given by

$$\begin{aligned} \frac{\partial^2 s_X(y)}{\partial x^2} &= -f''(x^*)\eta^{23}N^3|_* + 2\eta^{21}\eta^{12} \frac{\partial p^{12}}{\partial p^{21}} \frac{N^2|_*}{\det M} \left(\text{cofactor}_{r_{11}}(M) - \frac{N^1|_*}{N^3|_*} \text{cofactor}_{r_{13}}(M) \right) \\ &= f''(x^*)N^3|_* - 2k \frac{N^2|_*}{\det M} \left((p^{22}p^{33} - p^{23}p^{32}) - \frac{N^1|_*}{N^3|_*} (p^{22}p^{31} - p^{32}p^{21}) \right) \\ &= f''(x^*)N^3|_* + 2TN^3|_*, \end{aligned} \tag{45}$$

$$\frac{\partial^2 s_X(y)}{\partial y^2} = -f''(x^*)N^3|_*. \tag{46}$$

The evolutionary behaviour is described in Table 3. As above we know that $p^{22}p^{33} - p^{23}p^{32} > 0$ and $\det M < 0$ but the stability criteria for 3-species coexistence does not place any restriction on the sign or magnitude of $p^{22}p^{31} - p^{32}p^{21}$ and this can therefore be used to control the sign and magnitude of T . Thus, for different parameter combinations it is possible to generate all the evolutionary behaviour outlined in Table 3.

3. Discussion

In this study we have determined the adaptive dynamics of a general Lotka–Volterra system endowed not only with intraspecific parameter dependencies – modelling trade-offs – but also interspecific parameter dependencies – arising from the modelling of species interaction. We have developed general expressions for the fitness of a mutant strategy in a multi-species resident environment, the position of the singular strategy in such systems and the non-mixed second-order partial derivatives of the mutant fitness. Further analysis has shown how these derivatives can be written as an expression containing the derivatives of possibly interspecifically dependent

parameters with respect to the trade-off parameter (see (32,33) and Appendix A). We have proved in general that if the parameters related by the trade-off do not include such a dependent parameter then the possible evolutionary behaviour of the system is limited and the singular strategy can only be an evolutionary attractor or an evolutionary repeller. When the trade-off parameters do include a parameter that is interspecifically dependent it is possible to generate additional evolutionary behaviour and in particular evolutionary branching is possible. The type of behaviour expected depends on the curvature of the trade-off function.

The general relationship between the evolutionary behaviour and the curvature of the trade-off function can be interpreted in a more biologically intuitive manner using the rate of acceleration/deceleration of the costs implicit in the trade-off function. In Table 3 we outline the possible evolutionary behaviour depending on the relationship between $\eta^{\alpha\gamma} f''(x^*)$, 0 and T . The general results in this form show that branching requires the curvature of the trade-off to be above or below a threshold (set by T) depending on the sign of $\eta^{\alpha\gamma}$. It is also possible to express the behaviour, universally, in terms of the cost acceleration/deceleration implicit in the trade-off function. In particular the evolutionary behaviour can be characterised by whether the trade-off involves a ‘weakly’ accelerating or decelerating cost. To do this recall that for f to be a trade-off we require that $(\eta^{\alpha\gamma}/\eta^{\alpha\beta})f' < 0$. Since $p_{x_\alpha x_\beta}^{\alpha\beta}$ helps the growth rate when $\eta^{\alpha\beta}$ is positive, we define a benefit $B = \eta^{\alpha\beta} p_{x_\alpha x_\beta}^{\alpha\beta} = \eta^{\alpha\beta} x$. Since $p_{x_\alpha x_\gamma}^{\alpha\gamma}$ helps the growth rate when $\eta^{\alpha\gamma}$ is positive, we define a cost $C = -\eta^{\alpha\gamma} p_{x_\alpha x_\gamma}^{\alpha\gamma} = -\eta^{\alpha\gamma} f(x)$. Then $dC/dB = -(\eta^{\alpha\gamma}/\eta^{\alpha\beta})f'(x)$ so the trade-off condition is equivalent to a positive marginal cost. Furthermore, the cost acceleration $d^2C/dB^2 = -\eta^{\alpha\gamma} f''(x)$, which allows us to express all the results in Table 3 in terms of this quantity. For the singular point to be a branching point (which requires $0 > d^2C/dB^2 > -T$), we need a trade-off that is weakly decelerating in cost. If the trade-off is decelerating costly but not weakly so ($-\max(T, 0) > d^2C/dB^2$), the singular point is an evolutionary repeller. For Garden of Eden behaviour we require $0 < d^2C/dB^2 < -T$, that is a weakly accelerating cost. Finally, when the cost is accelerating but not weakly ($-\min(T, 0) < d^2C/dB^2$), we have an attractor. An immediate consequence of this is that branching points are not possible when $T < 0$ and Garden of Eden points are not possible when $T > 0$.

Thus the evolutionary behaviour can be classified universally in terms of the rate of acceleration/deceleration of the costs implied by the trade-off. This admits immediate biological interpretation. Of particular note is the result that evolutionary branching can only occur for a trade-off function corresponding (at the singular strategy) to weakly decelerating costs. We have therefore confirmed in general the findings from specific studies [11–13]. The importance of trade-offs in biological systems [9,10,15] make this a significant and testable finding.

The comparison of the systems with and without parameter dependencies also provides possible clues about the type of species interactions that are required for evolutionary branching. The fact that, for branching, the trade-off must ‘contain’ a dependent parameter indicates that speciation may require the evolving species to have a parameter coupling to another species. This type of coupling is typical of food chain systems (such as the predator–prey relationships in Examples 1 and 2) but may not be found in competitive interactions. This could have important implications for understanding the type of mechanisms that cause speciation.

Appendix A

If the parameters $p_{ij}^{\alpha\beta}$ in (14) are replaced by parameters $q_{ij}^{\alpha\beta}$ which can be composites of the (underlying) $p_{ij}^{\alpha\beta}$ then with the trade-off remaining as at (18) and $x = p_{x\alpha x\beta}^{\alpha\beta}, y = p_{y\alpha x\beta}^{\alpha\beta}$ still, the main results (21)–(23) then become, respectively

$$f'(x^*) = \frac{-\eta^{\alpha\beta} \left(\frac{\partial q_{x\alpha x\beta}^{\alpha\beta}}{\partial p_{x\alpha x\beta}^{\alpha\beta}} \right) N^{\beta*}}{\eta^{\alpha\gamma} \left(\frac{\partial q_{x\alpha x\gamma}^{\alpha\gamma}}{\partial p_{x\alpha x\gamma}^{\alpha\gamma}} \right) N^{\gamma*}} \tag{A.1}$$

and, provided that the composition is no more than linear in each variable,

$$\begin{aligned} \partial^2 s_X(y) / \partial x^2 \Big|_* &= -\eta^{\alpha\gamma} \left(\frac{\partial q_{x\alpha x\gamma}^{\alpha\gamma}}{\partial p_{x\alpha x\gamma}^{\alpha\gamma}} \right) f''(x^*) N^\gamma \Big|_* - 2\eta^{\alpha\gamma} \left(\frac{\partial q_{x\alpha x\gamma}^{\alpha\gamma}}{\partial p_{x\alpha x\gamma}^{\alpha\gamma}} \right) f'(x^*) \partial N^\gamma / \partial x \Big|_* \\ &\quad - 2\eta^{\alpha\beta} \left(\frac{\partial q_{x\alpha x\beta}^{\alpha\beta}}{\partial p_{x\alpha x\beta}^{\alpha\beta}} \right) \partial N^\beta / \partial x \Big|_*, \end{aligned} \tag{A.2}$$

$$\partial^2 s_X(y) / \partial y^2 \Big|_* = -\eta^{\alpha\gamma} \left(\frac{\partial q_{x\alpha x\gamma}^{\alpha\gamma}}{\partial p_{x\alpha x\gamma}^{\alpha\gamma}} \right) f''(x^*) N^\gamma \Big|_* . \tag{A.3}$$

We also find that (32) becomes

$$\begin{aligned} \frac{\partial N^\beta}{\partial p_{x\alpha x\beta C}^{\alpha\beta}} &= -\eta^{\beta\alpha} \sum_C \left(\frac{\partial q_{x\beta x\alpha}^{\beta\alpha}}{\partial p_{x\beta x\alpha C}^{\beta\alpha}} \frac{\partial p_{x\beta x\alpha}^{\beta\alpha}}{\partial p_{x\alpha x\beta}^{\alpha\beta}} s \right) N^\alpha \frac{\text{cofactor}_{\beta\beta}(M)}{\det M} \\ &\quad - \eta^{\gamma\alpha} \sum_C \left(\frac{\partial q_{x\gamma x\alpha}^{\gamma\alpha}}{\partial p_{x\gamma x\alpha C}^{\gamma\alpha}} \frac{\partial p_{x\gamma x\alpha}^{\gamma\alpha}}{\partial p_{x\alpha x\gamma}^{\alpha\gamma}} f'(x) \right) N^\alpha \frac{\text{cofactor}_{\gamma\beta}(M)}{\det M}, \end{aligned} \tag{A.4}$$

where the summations are over all underlying parameters appearing in the respective composites. There is a similar result for (33):

$$\begin{aligned} \frac{\partial N^\gamma}{\partial p_{x\alpha x\beta C}^{\alpha\beta}} &= -\eta^{\beta\alpha} \sum_C \left(\frac{\partial q_{x\beta x\alpha}^{\beta\alpha}}{\partial p_{x\beta x\alpha C}^{\beta\alpha}} \frac{\partial p_{x\beta x\alpha}^{\beta\alpha}}{\partial p_{x\alpha x\beta}^{\alpha\beta}} \right) \frac{\text{cofactor}_{\beta\gamma}(M)}{\det M} \\ &\quad - \eta^{\gamma\alpha} \sum_C \left(\frac{\partial q_{x\gamma x\alpha}^{\gamma\alpha}}{\partial p_{x\gamma x\alpha C}^{\gamma\alpha}} \frac{\partial p_{x\gamma x\alpha}^{\gamma\alpha}}{\partial p_{x\alpha x\gamma}^{\alpha\gamma}} f'(x) \right) N^\alpha \frac{\text{cofactor}_{\gamma\gamma}(M)}{\det M}. \end{aligned} \tag{A.5}$$

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