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Adaptive dynamics with vector-valued strategies

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ABSTRACT

Question: We examine strategy dynamics for evolutionary games with vector-valued strategies.

Mathematical methods: We use the fitness-generating function (*G*-function) to derive ESS maximum principle and strategy dynamics along multi-dimensional adaptive landscapes. We apply the dynamics to two models of co-evolution of competitors and one model of predator–prey co-evolution.

Results: When several traits evolve simultaneously (vector-valued strategies), a trait changes according to the product of each trait's fitness gradient and the matrix of covariances between the trait and the other traits. Only when these covariance terms are small does each trait in the strategy vector change in the direction of that trait's fitness gradient, similar to the scalar case. In the models, convergent stable points may be minima, maxima or saddle points. And the ESS may ultimately contain one, two or many species at distinct peaks of the adaptive landscape. The predator–prey model illustrates how the ESS strategy for the predator can result in an ESS for the prey that allows for any number of prey species to exist along a (flat) rim of a crater in the prey's adaptive landscape.

Key conclusions: In going from a scalar to a vector-valued strategy, the adaptive dynamics become more complicated with respect to fitness gradients, the bestiary associated with convergent stable points increases, the avenues for adaptive speciation and achieving an ESS increase, and the number of non-ESS species that can co-exist ecologically increases. By increasing the dimensionality of the adaptive surface, vector-valued strategies increase the opportunity for frequency-dependent selection to produce the number of species and the appropriate trait combinations for an ESS.

Keywords: adaptive dynamics, Darwinian dynamics, evolutionarily stable strategy, evolutionary game theory, tragedy of the commons, vector-valued strategy.

INTRODUCTION

The phenotype of an animal or plant is often best described by a number of distinct traits. For instance, insectivorous bats have traits that include: wing length, wing breadth, size and dimensions of the uropatagium (membrane connecting tail and hind-legs), dimensions of

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teeth, skull dimensions [mammalogists may measure between 5 and 25 cranial characters (Vaughn, 1978; Steppan and Sullivan, 2000)], length and characters of the digestive system, length and dimensions of the ear pinnae (external ear), and the frequency, duration, and amplitude of echo-locating sounds. The actual values for each of these traits often appear highly co-adapted. Consider a bat that attempts to capture slow-moving and highly manoeuvrable moths in flight. As in the case of bats of the family Mormoopidae, such a bat will have a short, broad wing (slow, inexpensive, and manoeuvrable flight), a large square uropatagium (serves as a glove for netting the moths in flight), and the capacity to produce high-frequency calls that can vary considerably in duration. Calls start high and drop sharply in frequency (calls of long duration seem to serve for scanning, while shorter calls permit fine-scale spatial resolution for pursuing insects). The bat's strategy is vector-valued where each component of the vector describes a different trait pertaining to wings, uropatagium, sound-emitting capability, and ear morphology. Organisms are vectors of traits. Here, we use aspects of evolutionary game theory that allow one to model the evolution of multiple traits simultaneously.

If the strategy set is discrete, then the evolutionary game can be represented in matrix form such as the 'Hawk' and 'Dove' strategies from the game of chicken (see Maynard-Smith, 1982). For quantitative traits such as body size in animals, wing dimensions in flying organisms, or resource allocation strategies in plants and animals, the strategy set is continuous. Furthermore, organisms are best described by combinations of traits.

Evolutionary game theory and the concept of evolutionarily stable strategies (Maynard-Smith and Price, 1973) provide a framework for predicting the outcomes of natural selection (Vincent and Brown, 1988). An important development has been an understanding of adaptive dynamics (*sensu* Metz *et al.*, 1996; Abrams, 2001). Natural selection has an ecological dynamic involving changes in population size, and an evolutionary dynamic involving changes in the strategy value or strategy composition of the population. We will refer to the former as the population dynamics and the latter as the strategy dynamics. Together, the population and strategy dynamics comprise the Darwinian dynamics of natural selection (Vincent and Brown, 2005). In Table 1 we define a set of terms and concepts that will be useful for the remainder of this paper. We will highlight the first use of these terms in italics. While these definitions may not always conform to common usage, they help fix and clarify the concepts to follow.

In a manner similar to dynamics from quantitative genetic models (Charlesworth, 1990), the rate of change in the value of an evolutionary *strategy* (as given by the *strategy dynamics*) is proportional to the slope of the *adaptive landscape* multiplied by an evolutionary speed term (Vincent, 1990; Abrams *et al.*, 1993a; Geritz *et al.*, 1998). The latter has been shown to be a function of heritability and additive genetic variance (Vincent *et al.*, 1993). Dieckmann and Law (1996) and Leimar (in press) derive a strategy dynamic for vector-valued strategies for fitness functions involving a mutant strategy played against a common strategy within the population. Vukics *et al.* (2003) apply this dynamic to investigate evolutionary branching and adaptive speciation for vector-valued strategies. The fitness-generating function or *G*-function refines the notion of having a small sub-population of individuals with a mutant strategy within a population with some other strategy. Rather than have a separate fitness function for the mutant and resident strategies, the *G*-function considers the strategy of any focal individual to be influenced by its strategy and the strategies of others. While the *G*-function concept as developed in Vincent and Brown (1984) for modelling evolutionary games does not preclude multi-dimensional strategies (Vincent and Brown, 1987a, 1987b, 2005), we have not provided many examples. Increasing the dimensionality of strategies opens up new possibilities for the

Table 1. Definitions of terms and concepts used in this paper

Trait	A trait is a particular characteristic of an individual that is inherited from its parent(s), e.g. wing length, wing width, body mass
Phenotype	Phenotype is defined by a set of traits whose values are unique within a species, e.g. it may be sufficient to describe a bird species by the ratio of its wingspan to its wing width and by its weight. Thus, an individual that has a significantly different value (on one or more of these traits) from other members of the population is classified as a phenotype
Strategy	The set of trait-values for a single individual. A strategy might influence the individual's fitness or the fitness of others
Species	A species is defined as a collection of individuals that interbreed. The set of phenotype strategy values within a species describe a distribution around the species' mean
Population dynamics	Population dynamics describe changes in the population densities of species over time. This process is usually modelled with first-order ordinary differential equations or difference equations
Strategy dynamics	Adaptive dynamics describe the change in the mean and distribution of strategy values of a species over time. This process is usually modelled with first-order ordinary differential equations or difference equations
Darwinian dynamics	Evolutionary dynamics includes both population dynamics and adaptive dynamics
Adaptive space	The multi-dimensional space of all possible strategy values that a focal individual can possess. This space is a Cartesian product of traits
Adaptive landscape	The adaptive landscape defines the expected fitness of a focal individual as a function of its strategy value. It is a surface in the adaptive space with the addition of an axis for fitness. Evolutionary dynamics determine the shape of the landscape. You may think of the adaptive landscape as a blanket in a three-dimensional space whose shape changes with temporal changes in the population sizes and mean strategy values of species

outcomes of strategy dynamics (Vukics *et al.*, 2003; Leimar, in press), the path by which strategies evolve towards an evolutionarily stable strategy (ESS), the numbers and kinds of *species* that can co-exist at an ESS or non-ESS points, and the phenotypic dimensions along which niche co-evolution occurs between species.

Within evolutionary game theory, the tools for considering the outcome of natural selection acting on a single trait are well developed. A fitness-generating function (G-function) (Vincent and Brown, 1984, 1988) describes expected fitness to an individual as a function of its strategy, the strategies of others, the frequency of extant strategies within the population (frequency-dependence), and population size (density-dependence). The mean strategy value of the population changes in the direction of the slope of the adaptive landscape. As the strategy of the population 'climbs' the landscape, the landscape itself may be rising or falling with changes in population size, or changing shape in response to changes in strategy frequencies. In response to these adaptive dynamics, the population may come to rest at an evolutionarily stable maxima, minima or saddle point. If a global maximum of the adaptive landscape exists, then the strategy may be an ESS. To be an ESS, such a strategy must be resistant to invasion by rare alternative strategies and be convergent stable in that dynamical changes in the values of strategies (referred to as strategy dynamics) will return the population's strategy to the ESS in response to small perturbations in strategy values and/or frequencies (Cohen *et al.*, 1999).

A point may be an evolutionarily stable minima (Abrams *et al.*, 1993b) in the sense that it is convergent stable but not resistant to invasion. Strategy dynamics can evolve to such a point. But, once at such a minimum the population's strategy value may 'speciate' into two values that climb either side of the valley in the adaptive landscape (Brown and Pavlovic, 1992; Vincent *et al.*, 1993; Metz *et al.*, 1996; Geritz *et al.*, 1998; Dieckmann and Doebeli, 1999). Pairs of strategy values may then evolve to multiple peaks in the landscape (e.g. an ESS with several strategies) or to minima that permit additional speciation or bifurcation events that produce additional extant strategies. Here we will examine similar events with vector-valued strategies.

In what follows, we consider explicitly the *G*-function when the strategy is continuous and vector-valued. A vector-valued strategy produces a multi-dimensional adaptive landscape whose surface has the same dimensionality as the number of components (= traits) in the strategy. In general, adaptive dynamics on one trait are influenced by the fitness gradients of all components, adjusted for covariances among the strategy components (Leimar, in press). In most cases, however, we expect strategy dynamics to reduce to each component changing in the direction of its fitness gradient. However, unlike strategy dynamics for a scalar-valued strategy, the gradient of the landscape with other strategy components can influence the direction and rate of change of any given component. In a manner like quantitative genetics models of evolution, the magnitude and direction of evolution on each trait is influenced by the matrix of phenotypic covariances among the different traits within the population (Dieckmann and Law, 1996).

We will consider the outcomes of strategy dynamics in terms of resistance to invasion and the convergence stability of particular strategies on the adaptive landscape. Most of the concepts and principles that apply to scalar-valued strategies extend to vector-valued strategies (Vincent and Brown, 2005). Here we extend an earlier evolutionary game modelled on Lotka-Volterra competition (Brown and Vincent, 1987c; Vincent *et al.*, 1993) to include a vector-valued strategy. To consider an evolutionary game with two separate *G*-functions, we extend a predator–prey model (Brown and Vincent, 1992) to include vector-valued strategies. Under vector-valued strategies, the ESS concept, the ESS maximum principle, and Darwinian dynamics permit more sophisticated games of character evolution, produce a richer array of evolutionary phenomena, and consider explicitly how natural selection produces co-adapted suites of traits within individual organisms.

OUTCOMES OF EVOLUTIONARY DYNAMICS

The ESS concept (Maynard-Smith and Price, 1973) provides evolutionary game theory with a solution concept for identifying possible outcomes of natural selection. Do the *Darwinian dynamics* result in strategies that are ESS? It depends upon the ESS definition. Maynard-Smith (1982) originally described an ESS as a strategy or set of strategies, which, when common, cannot be invaded by any rare alternative strategies. This property of an ESS can be stated in terms of the ESS maximum principle (Vincent and Brown, 1988). This principle ensures that a population at an ESS is resistant to invasion. But as noted by several authors (Taylor and Jonker, 1978; Hines, 1980; Eshel, 1983, 1996; Takada and Kigami, 1991; Kisdi and Meszena, 1994; Metz *et al.*, 1996; Taylor and Day, 1997), resistance to invasion does not ensure that the Darwinian dynamics will yield an ESS. When strategy values and strategy frequencies are perturbed slightly from an equilibrium solution, the Darwinian dynamics may not return the strategies to the equilibrium point. In this case, the equilibrium is not a likely outcome of evolution by natural selection and one can hardly expect to observe it in Nature. To be useful, an ESS must not only be resistant to invasion by individuals who possess rare alternative strategy values (= mutants), but it must also be convergent stable. The Darwinian dynamics must return strategy values back to the ESS in response to perturbations. If the return to ESS occurs only with small perturbations of strategy values from their ESS values, then there is local convergence stability. If the return occurs after any perturbation size, then there is global convergence stability. For the ESS, we have used a definition that requires an ESS to be resistant to invasion and convergent stable (see Cohen *et al.*, 1999). Maintaining these properties in the definition serves three purposes. First, it updates the ESS concept by integrating evolutionary dynamics with the likely outcomes of evolution by natural selection. Second, it reduces the need for a confusing proliferation of terms to describe points that have subsets of convergence stability and resistance to invasion. Third, over an ale in Sussex, the late Maynard Smith indicated a preference for keeping the ESS definition abreast of current knowledge (personal communication).

The ESS maximum principle

To develop a *G*-function, one begins with any model of population dynamics. Next, one specifies an evolutionary strategy, $\mathbf{u}$, that may be scalar or vector-valued. This strategy must belong to some set of evolutionarily feasible strategies, $\mathcal{U}$, where the set is determined by physical, genetic, and biophysical constraints. Finally, one specifies explicitly or implicitly how the strategy value of a focal individual, $\mathbf{v}$, the strategies of others, $\mathbf{u}$, and the population sizes of each of the extant strategies, $\mathbf{x}$, influence an individual's expected per capita growth rate (differential equation model) or finite growth rate (difference equation model). The fitness-generating function takes the form of $G(v, \mathbf{u}, \mathbf{x})$. Below, we formalize three aspects of evolutionary games with vector-values strategies. First, the development of a fitness-generating function that describes how the population sizes of each strategy change with time. Second, the formal definition of an ESS as a strategy or set of strategies that cannot be invaded by rare alternative strategies and which is convergent stable. Third, the ESS maximum principle that states how, at an ESS, each strategy of the ESS must maximize fitness and hence reside on peaks of the adaptive landscape (defined as the plot of fitness versus the strategy of the focal individual: G versus v). For the following development, we will assume that different strategies represent different species.

The following definitions and theorm apply equally well to scalar- or vector-valued strategies (Brown and Vincent, 1987b; Vincent *et al.*, 1993; Cohen *et al.*, 1999). Here, we reiterate our ESS definition and the ESS maximum principle (Vincent *et al.*, 1996; Vincent and Brown, 2005).

Let $\mathbf{u} = [\mathbf{u}_1, \ldots, \mathbf{u}_{n_s}]^{\mathrm{T}}$ be the vector of strategies found among s species in the community. Let each strategy vector $\mathbf{u}_i$, $i = 1, \ldots, n_s$ have the same number of components n_u; i.e. $\mathbf{u}_i = [u_{i1}, \ldots, u_{in_u}]^{\mathrm{T}}$. Let $\mathbf{x} = [x_1, \ldots, x_{n_s}]^{\mathrm{T}}$ be the vector of population densities where x_i is the population size of the species using strategy $\mathbf{u}_i$ for species $i = 1, \ldots, n_s$. To be biologically sensible, population sizes $\mathbf{x}$ must lie in the non-negative orthant

$$\mathcal{O}^{n_s} = \{\mathbf{x} \in \mathcal{R}^{n_s} \mid \mathbf{x} \geq 0\}$$

where $\mathbf{x} \geq 0$ means that at least one population size of the vector $\mathbf{x}$ is greater than 0.

The population dynamics for a community that can be represented by a single G-function is given by

$$\dot{x}_i = x_i G(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)|_{\mathbf{v}=\mathbf{u}_i}.$$

In what follows, we assume that for any $\mathbf{u} \in \mathcal{U}$ there exists an equilibrium solution $\mathbf{x}^*$ satisfying

$$x_i^* G(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)|_{\mathbf{v}=\mathbf{u}_i} = 0, \quad i = 1, \ldots, n_s.$$

Here $\mathcal{U}$ denotes the set of feasible strategies. If for some i, the equilibrium condition is satisfied by the solution $x_i^* G(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)|_{\mathbf{v}=\mathbf{u}_i} = 0$ with $\mathbf{x} \geq 0$, then the equilibrium solution is called an **ecological equilibrium point**. We reorder the i index, if necessary, so that all $x_i > 0$ are listed first. Thus, at an ecological equilibrium point there exists a $\sigma \geq 1$ such that the equilibrium solution is given by

$$\begin{aligned} &G(\mathbf{v}, \mathbf{u}, \mathbf{x}^*)|_{\mathbf{v}=\mathbf{u}_i} = 0 \text{ with } x_i^* > 0 \quad &&\text{for} \quad i = 1, \ldots, \sigma \\ &x_i^* = 0 &&\text{for} \quad i = \sigma + 1, \ldots, n_s \end{aligned} \tag{1}$$

We designate the strategies corresponding to the non-trivial solutions as

$$\mathbf{u}_c = [\mathbf{u}_1, \ldots, \mathbf{u}_\sigma]^{\mathrm{T}}$$

and the remaining strategies as

$$\mathbf{u}_m = [\mathbf{u}_{\sigma+1}, \ldots, \mathbf{u}_{n_s}]^{\mathrm{T}}.$$

For the definition that follows we will require certain properties that are similar to asymptotic stability for the ecological equilibrium point. We cannot assume that $\mathbf{x}^*$ is asymptotically stable at the onset, since $\mathbf{x}^*$ will, in general, lie on the boundary of $\mathcal{O}^{n_s}$ and trajectories starting at neighbouring points not in $\mathcal{O}^{n_s}$ are of no interest and need not approach $\mathbf{x}^*$. Rather, we require that every trajectory starting in $\mathcal{O}^{n_s} \cap \mathcal{B}$ where $\mathcal{B}$ is an open ball about $\mathbf{x}^*$ remains in $\mathcal{O}^{n_s}$ for all time and converges to $\mathbf{x}^*$ as $t \to \infty$. An ecological equilibrium point that satisfies these properties is called an ‘ecologically stable equilibrium point’ (ESE). If $\mathcal{B}$ can be made arbitrarily large, then $\mathbf{x}^*$ is said to be a global ESE, otherwise it is a local ESE. These considerations ensure that the ESE consists of positive population densities.

Definition 1. *The vector* $\mathbf{u}_c \in \mathcal{U}$ *is an ESS for the ecological equilibrium point* $\mathbf{x}^* \in \mathcal{O}^{n_s}$ *if, for any* $n_s \geq \sigma$ *and any* $\mathbf{u}_m \in \mathcal{U}$, $\mathbf{x}^*$ *is an ecologically stable equilibrium point.*

The ESS definition requires that an ESS cannot be invaded by one or more alternative species. These alternative species need not use strategies near those used by members of the coalition. In this sense, the ESS is always global with respect to $\mathcal{U}$. As an ESS, the ESE becomes a stable equilibrium point for any $\mathbf{x}$ near $\mathbf{x}^*$ regardless of the increased dimension of $\mathbf{x}$ and $\mathbf{u} = [\mathbf{u}_c, \mathbf{u}_m]$. Thus, according to the above definition, an ESS is not only uninvadable (like Maynard Smith’s original definition) but it must also be convergent stable. If $\mathbf{x}^*$ is a local ESE, then the alternative species must be rare. If $\mathbf{x}^*$ is a global ESE, then the invading species need not be rare.

The ESS maximum principle expresses the aspect of the ESS which is optimal. An ESS strategy may be thought of as optimal to an individual in the sense that it maximizes its fitness given the current biotic environment. However, an ESS is not optimal in the sense of maximizing fitness with respect to the species' strategies.

Theorem 1 (ESS maximum principle). *If* $\mathbf{u}_c = [\mathbf{u}_1^*, \ldots, \mathbf{u}_\sigma^*]$ *is an ESS for the ecological equilibrium point* $\mathbf{x}^* \in \mathcal{O}^{n_s}$*, then* $G(\mathbf{v}, \mathbf{u}^*, \mathbf{x}^*)$ *must take on its maximum value as a function of* $\mathbf{v} \in \mathcal{U}$ *at* $\mathbf{v} = \mathbf{u}_1^*, \ldots, \mathbf{u}_\sigma^*$. *Furthermore*, $\max G(\mathbf{v}, \mathbf{u}^*, \mathbf{x}^*) = 0$.

According to the ESS maximum principle, each strategy of an ESS must be a global (with respect to $\mathbf{v} \in \mathcal{U}$) maximum of the adaptive landscape. This maximum ($= 0$) is achieved at $[\mathbf{u}^*, \mathbf{x}^*]$. The definitions and theorem above provide the necessary conditions for ensuring that $\mathbf{u}^*$ is resistant to invasion by any $\mathbf{u} \in \mathcal{U}$. The ESS maximum principle simply formalizes the original idea of Maynard Smith. If a strategy of an ESS did not maximize fitness at the ESS, then whatever non-ESS strategy has higher fitness would be able to invade. This contradicts the invasion-resistant property of an ESS.

Convergence stability and the outcomes of evolutionary dynamics

Adding to the above definition of an ESS, $\mathbf{u}^*$ must also be convergent stable. It is a stability property of the evolutionary dynamics. The conditions for invasion resistance need not be the same as those for convergence stability. Necessary conditions for convergence stability have been derived for scalar-valued strategies and communities composed of a coalition of one species (Abrams *et al.*, 1993b; Metz *et al.*, 1996), and it is tempting to extend these conditions to vector-valued strategies. However, whereas the ESS maximum principle extends easily from scalar-valued to vector-valued strategies, the conditions for convergence stability do not. Even for scalar-valued strategies, the conditions for convergence stability magnify in complexity in going from an ESS of one to an ESS of two species (Cohen *et al.*, 1999). The conditions for the convergence stability of vector-valued strategies are even more complicated (Vukics *et al.*, 2003; Leimar, in press).

The Darwinian dynamics and ESS maximum principle provide two means of finding and verifying candidate ESS solutions. First, one can use strategy dynamics to find points of convergence stability, and then inspect the resulting adaptive landscape to verify that $\mathbf{u}^*$ satisfies the ESS maximum principle. Second, one can use the necessary conditions of the ESS maximum principle to find candidate solutions. Inspection of the adaptive landscape at these candidate solutions can be used to verify that the ESS maximum principle has indeed been fulfilled; i.e. that the values of the G-function at its maximum are zero. Strategy dynamics, applied to small or large perturbations of strategy values around the candidate solutions, can be used to verify convergence stability. With strategy dynamics, the strategies of different species may often converge on a common value. In such cases, it may be convenient and biologically realistic to drop one of the species (when and if its population size becomes sufficiently small) or to merge the species into a single species when their strategy values become so close as to represent no more than within-species phenotypic variation.

Combinations of strategies among the extant species can be convergent stable without being ESS. Obviously, strategy dynamics can take the community to maxima of the adaptive landscape that are local but not global with respect to $\mathbf{v} \in \mathcal{U}$. Such a strategy may be convergent stable but it cannot resist invasion from those strategies with fitnesses higher than the current local maximum. If $\mathbf{u}$ comes to rest at a local maximum that is not also a global maximum of the adaptive landscape, then it is not possible for adaptive dynamics alone to shift **u** to points of higher fitness, or to an ESS. Escape from a local maximum of the adaptive landscape requires the invasion of novel species with strategies quite distant from those of the existing species. As noted by Wright (1931), it is hard to evolve away from a local maximum, even under the additional flexibility in landscape dynamics afforded by frequency-dependence (Cohen *et al.*, 1999).

Points that appear as minima on the landscape may be convergent stable (Brown and Pavlovic, 1992), and represent the evolutionarily stable minima (Abrams *et al.*, 1993b). Both means of finding ESS candidate solutions can be used to identify these evolutionarily stable minima. For instance, strategy dynamics on a fixed number of species can converge on these points because, under frequency-dependence, the minimum does not appear as such until it is achieved by the Darwinian dynamics. Or, application of the first-order necessary conditions of the ESS maximum principle may identify extreme points that are minima rather than maxima, and subsequent perturbation analyses of these using strategy dynamics may reveal convergence to the minimum.

Under vector-valued strategies, a variety of points may be convergent stable without being local or global maxima of the landscape. For **u** on the interior of the strategy set, these points may be a minimum with respect to all components of the strategy, or saddle points where the gradients along strategy components are positive for some and negative for others. These points, while convergent stable, are not resistant to invasion, and in fact are not resistant to invasion by species with strategies arbitrarily close to the extant species' strategy. Such convergent-stable, non-ESS points are easy to escape from via adaptive speciation (Brown and Pavlovic, 1992; Geritz *et al.*, 1998; Geritz, 1998; Cohen *et al.*, 1999; Dieckmann and Doebeli, 1999). The current species can be split into two daughter species with very similar yet distinct strategies, or a new species can be introduced with a strategy arbitrarily close to the existing one. In either case, the two species will begin diverging from each other as they evolve up opposite slopes of the adaptive landscape. In time, these strategies may achieve an ESS, or evolve to other convergent-stable minima or saddle points. In this way, a community that begins with fewer species than that of an ESS can evolve via Darwinian dynamics to minima or saddle points, speciate, and progress further towards the ESS number of species and strategy values (Cohen *et al.*, 1999).

EVOLUTIONARY GAMES WITH VECTOR-VALUED STRATEGIES

The Darwinian dynamics include both changes in species' population densities (*population dynamics*) and species' mean strategy values (*strategy dynamics*). The *G*-function is central to both dynamics. In the Appendix we derive how the gradient of the *G*-function influences the direction and magnitude of evolutionary change. The following dynamics conform to results obtained in expression 6.1 of Dieckmann and Law (1996), and the general evolutionary dynamics derived by Vukics *et al.* (2003) and Leimar (in press). Under the assumptions given in the Appendix, we obtain the following strategy dynamic:

$$\dot{\mathbf{u}}_i = \mathfrak{D}_i \left.\frac{\partial G}{\partial \mathbf{v}}\right|_{\mathbf{u}_i},$$

where $\mathfrak{D}_i$ is a variance matrix for species i. The variance matrix is square and has as many rows and columns as there are different traits in the strategy. The trace of $\mathfrak{D}_i$ gives the variance in strategy values found among individuals of a given species. Each element of the diagonal describes the extant variability surrounding a separate component of the strategy vector. The off-diagonal elements of $\mathfrak{D}_i$ give the covariance between strategy values for different traits within the strategy. For instance, the element d_{ijk} describes the covariance between the values of trait j and the values of trait k found among individuals within the population x_i.

The variance matrix $\mathfrak{D}_i$ contributes towards strategy dynamics in the same manner as the variance–covariance matrix of quantitative genetic models. However, there are some important differences. The matrix $\mathfrak{D}_i$ is a phenotypic covariance matrix, not a genetic covariance matrix. Whatever covariances emerge from the adaptive dynamics are due to co-adaptations among traits, and not due to mechanisms such as genetic linkages. This covariance matrix results from the strategy climbing the adaptive landscape along diagonals, and not parallel to any of the trait axes. The phenotypic covariance matrix is dynamic. Vincent *et al.* (1993) developed the variance dynamics. When an ESS is reached, the phenotypic matrix no longer changes. Cohen and Vincent (1997) suggested that lack of changes in the covariance values in the phenotype matrix may indicate that populations are near (or at) an ESS. Furthermore, one can expect that any genetically related covariance among traits contributes additively to the phenotypic covariances. (Of course, genetic and physical constraints and fixed non-independences among traits can be built into the model as equality or inequality contraints.)

Because of interbreeding or heritable independence among the strategy components, the covariance terms within a species should be small. As the species approaches the ESS, the direction of approach that might have contributed to coadaptive covariances will become transitory. At the ESS, the covariance terms should vanish. Furthermore, the adaptive dynamics emerge from a summation of all the covariance terms multiplied by the respective fitness gradients. The contribution of the covariance terms to adaptive dynamics may even cancel each other out because of the summation of both positive and negative terms. When the covariance terms are sufficiently small, the adaptive dynamics for each component of species i's strategy vector, $\mathbf{u}_i$, is simply given by:

$$\dot{u}_{ik} = \sigma_{ik} \left. \frac{\partial G}{\partial v_k} \right|_{\mathbf{u}_i}$$

for $k = 1, \ldots, n_u$.

LOTKA-VOLTERRA COMPETITION

Lotka-Volterra competition equations provide a useful means for transforming an ecological model of population dynamics into an evolutionary game (Roughgarden, 1976; Brown and Vincent, 1987a; Charlesworth, 1990; Abrams *et al.*, 1993b; Vincent *et al.*, 1993; Metz *et al.*, 1996; Cohen *et al.*, 1999). Previous works have introduced a scalar-valued strategy that influences carrying capacity and the competition coefficient. In these models, carrying capacity, K, is a function of the individual's strategy, whereas the competition coefficient, α, is assumed to be a function of the individual's strategy and the strategy of others. With a scalar-valued strategy, Lotka-Volterra models can produce evolutionary games that have one, several or many different strategies (= species) at the ESS. When the community begins with a fewer number of species than required for the ESS, adaptive dynamics may take a species to an evolutionarily stable minima (Abrams *et al.*, 1993b; Vincent *et al.*, 1993), at which point competitive speciation (Rosenzweig, 1978) or sympatric speciation (Thoday and Gibson, 1962, 1970; Maynard-Smith, 1966) produces daughter species that evolve up the respective slopes of the adaptive landscape. Adaptive dynamics in conjunction with adaptive speciation can attain the ESS (Cohen *et al.*, 1999). Alternatively, adaptive dynamics in Lotka-Volterra models can move strategies to local evolutionary maxima. At these points, competitive speciation is less likely, and evolution towards the ESS more difficult.

In the following two models, we extend previous modelling of co-evolution and speciation by introducing a vector-valued strategy. In the first model, we introduce a second component to the strategy as a term in an evolutionary tragedy of the commons (Hardin, 1968). The second component has no direct effect on competitive interactions among species, on the co-evolution of species or on speciation itself. Rather, it introduces a bit of an arms race where more extreme is better, but at a price to the individual and the population. The adaptive landscape is particularly flexible with respect to changes in strategy frequencies along the axis of the first strategy component, but it is relatively rigid along the axis of the second component. The model serves to illustrate evolution along a two-dimensional adaptive landscape and shows the influence of each strategy component on the other component's value and evolution.

In the second model, we make carrying capacity and the competition coefficients functions of each of two strategy components. The two components can co-adapt to influence the number of species at the ESS, the outcomes of evolution when the number of strategies is fixed below the number of the ESS, and the opportunities for adaptive speciation. In this model, the adaptive landscape is particularly labile along both axes of strategy components and in response to the number of species and the value of each species' strategy. Of particular interest is whether the additional avenues for adaptive ascent increase or decrease the likelihood of natural selection attaining an ESS.

Tragedy of the commons in a Lotka-Volterra model

Here we use Lotka-Volterra competition models as an example of Darwinian dynamics and ESSs when species possess vector-valued strategies. We use a Lotka-Volterra competition model to describe a species per capita growth rate. We let the vector-valued strategy have two components. The first component influences carrying capacity, K, and competition coefficients, α, in the same way as in Vincent *et al.* (1993) and Cohen *et al.* (1999). An individual's carrying capacity fits a Gaussian curve with respect to the first component of its strategy, v_1. Carrying capacity takes on a maximum value at $v_1 = 0$. The 'variance' of this curve, σ_k^2, determines the severity with which an individual loses carrying capacity as its first strategy component deviates from $v_1 = 0$. With a larger 'variance', the Guassian curve is flatter and the individual suffers less from a deviation. The term σ_k^2 is a scaling term that determines the flatness of the Gaussian curve. The competition experienced by an individual from another species (including its own) is influenced by the difference between the first component of the individual's strategy and the first component of the species' mean strategy. In addition, we add a factor β that describes the level of asymmetry in competition. When $\beta > 0$, an individual with a larger value for v_1 has a larger negative effect on an individual with a smaller v_1 than the smaller value has on the larger. The competition function follows a Gaussian curve with respect to v_1 and this function takes on a maximum at β. Furthermore, the competition coefficient, by means of an additive adjustment term, takes on a value of one when individuals share the same value for the first component. The 'variance' of the function of competitive effects, σ_α^2, determines how quickly the competition coefficient changes as competitors deviate in their strategy values for the first component. A large variance means that the competition coefficient changes slowly with changes in v_1. Again, the term σ_α^2 is a scaling term that determines how flat the Gaussian competition curve is with respect to deviations of the individual's strategy from the strategy of a population.

We let the second component of an individual's strategy, v_2, influence carrying capacity and the competition coefficients via a 'bully' function, B. This bully function describes any form of competition in which being slightly larger than your neighbour confers a competitive advantage by reducing the negative effects of others and increasing one's own negative effect on others. Height in trees provides an obvious example. Being taller than one's neighbour increases one's own access to light at the expense of shorter individuals that are now shaded. This favours a kind of arms race in which trees gain by evolving a height advantage against neighbours. However, this advantage is nullified as soon as others adopt a taller height. But, this arms race has a price. While the total amount of available sunlight remains unchanged whether the trees are short or tall, all of the trees must now produce and support the non-productive woody trunk that produces height. This reduces the availability of resources for productive tissues such as roots, stems, and ultimately seeds. In trees via tree trunks, competition for light produces a tragedy of the commons (Hardin, 1968). The advantage for being taller than one's neighbours provides a small individual benefit that is smaller than the collective loss. And this small advantage is eliminated as soon as others evolve a similar height; but the collective cost remains.

As a tragedy of the commons, we let the bully function, B, scale the competitive effect that others have on you. If another is larger than you with respect to v_2, then its negative effect on you is amplified; if smaller, then its negative effect is diminished. When individuals share the same value for v_2, then $B = 1$ and the effect of the bully function on the competition coefficient vanishes. But, the individual pays a price in terms of its own carrying capacity for increasing v_2. An individual loses carrying capacity proportional to $(1 - v_2^2)$. This effect and functional form effectively restricts the reasonable values for this second component to $v_2 \in [0, 1)$. The function B and its effect on the competition coefficients introduces an evolutionary arms race: bigger values for v_2 are better for competition and expensive in terms of K.

In the following functions for G, K, α, and B, both components of an individual's strategy influence its fitness via effects on competition coefficients and carrying capacity. The two components do this in very different ways. The first component has an interior value for v_1 that maximizes carrying capacity (introduces stabilizing selection) and competition is minimized by having v_1 much larger or much smaller than one's competitors (introduces elements of disruptive selection). The second component, v_2, is under directional selection to be larger with respect to competition and under directional selection to be smaller with respect to carrying capacity. In terms of the G-function, the model is given by

$$G(\mathbf{v}, \mathbf{u}, \mathbf{x}) = \frac{R}{K(\mathbf{v})} \sum_{j=1}^{r} \alpha(\mathbf{v}, \mathbf{u}_j)\, x_j$$

$$K = (1 - v_2^2)\, K_{\max} \exp\left(-\frac{v_1^2}{2\sigma_k^2}\right)$$

$$\alpha(\mathbf{v}, \mathbf{u}_j) = 1 + B \exp\left[-\frac{(v_1 - u_{j_1} + \beta)^2}{2\sigma_\alpha^2}\right] - \exp\left[-\frac{\beta^2}{2\sigma_\alpha^2}\right]$$

$$B = 1 + B_{\max}(u_{j_2} - v_2).$$

Example 1

For the first example, we started with a single species with $\mathbf{u}_1(0) = (0,\ 0)$ and an initial population of $N = 100$. Thereafter, we let Darwinian dynamics determine changes in $\mathbf{u}_1$ and the fitness-generating function evaluated at $\mathbf{v} = \mathbf{u}_1$ to determine changes in population size, x. We set the model's parameters equal to the following values:

$$\begin{aligned} K_{\max} &= 100 \\ R &= 0.25 \\ \sigma_\alpha &= 2 \\ \sigma_k &= \sqrt{2} \\ \beta &= 2 \\ B_{\max} &= 1 \end{aligned}$$

Under Darwinian dynamics, the single species' strategy and population size converge on the following values:

$$\begin{aligned} x^* &= 84.0912 \\ \mathbf{u}^* &= [0.6064 \quad 0.2796]. \end{aligned}$$

Figure 1 illustrates that this solution satisfies the ESS maximum principle and we conclude that the model has an ESS coalition of one species. At the ESS, the species has a population size that is less than it would have had at $\mathbf{u} = (0,\ 0)$. When both strategy components equal zero, $x^* = K_{\max} = 100$. Evolution in each of the components results in the species sacrificing

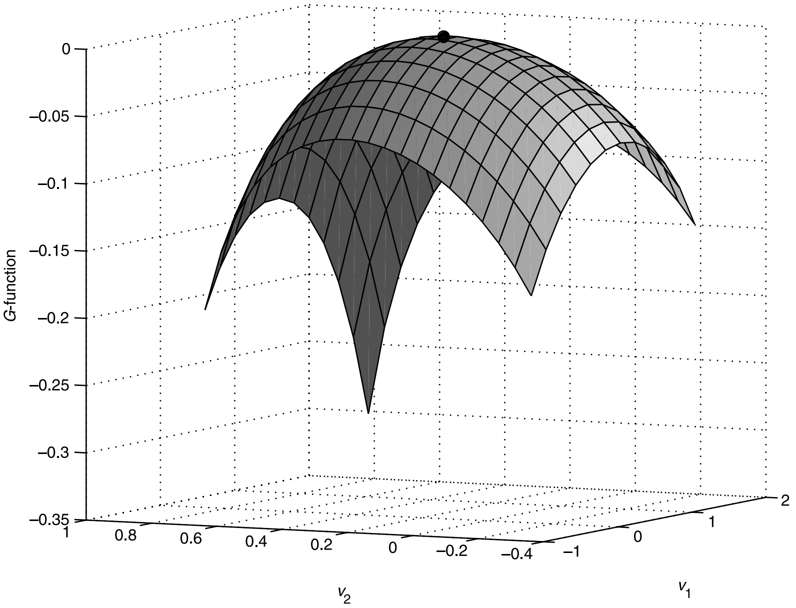

Fig. 1. An ESS coalition of one species. Regardless of the number of starting species or their initial strategy values, adaptive dynamics results in the single-strategy ESS.

equilibrium population size at the ESS. In terms of the first strategy component, the asymmetry in the competition coefficient favours larger values for v_1. In terms of the second strategy component, the bully function produces the tragedy of the commons: $v_2^* > 0$.

The ESS appears to be global with respect to convergence stability and with respect to the number of species. Regardless of the starting value for the species' strategy, Darwinian dynamics evolve to $\mathbf{u}^*$. If one begins with several species, the strategies of all of the species eventually evolve towards the same peak.

Ecologically, we have been able to get as many as three species to co-exist in the neighbourhood of the peak of the ESS. This can happen only if the peak itself is unoccupied by a species. In contrast, when the strategy has just one component (scalar-valued), at most two species can co-exist in the neighbourhood of a peak. This means that more species can co-exist within a non-ESS community, before it evolves to an ESS. And the number of additional species that can co-exist increases with the dimensionality of the strategy.

Example 2

Next, we increase the variance term of K. Increasing σ_k reduces the stabilizing selection of K when $v_1 = 0$, and it reduces directional selection towards $v_1 = 0$ when an individual's value for v_1 deviates from 0. If the second component of the strategy is set equal to zero (making the strategy scalar-valued), increasing σ_k changes the ESS from a single species to two or more species (Vincent *et al.*, 1993; Cohen *et al.*, 1999). As before we start with a single species with $\mathbf{u} = (0, 0)$ and $x^* = 100$. We leave all of the parameters unchanged save for increasing σ_k to $\sqrt{8}$. Darwinian dynamics result in the following convergent-stable solution (Fig. 2):

$$x^* = 63.8166$$

$$\mathbf{u}^* = [2.4261 \quad 0.2796].$$

This solution is at a local maximum point of the adaptive landscape. But, it is not an ESS. The G-function is greater than zero elsewhere, and the solution is susceptible to invasion. The convergent stability of this solution can be verified by starting the system with two species, $n_x = 2$, in the neighbourhood of this local maximum and noting that the dynamics return to the same peak with the two species using the same strategy, $\mathbf{u}^*$.

If we start the system with two species, $n_x = 2$, with strategy values far enough away from the local maximum

$$\mathbf{x}(0) = [14.4890 \quad 60.9888]^{\mathrm{T}}$$

$$u_1(0) = [-1.2 \quad 0.3]^{\mathrm{T}}$$

$$u_2(0) = [2.3 \quad 2.6]^{\mathrm{T}},$$

then under strategy dynamics, we obtain

$$x^* = [13.6857 \quad 61.7222]^{\mathrm{T}}$$

$$u_1^* = [-1.2039 \quad 0.3025]^{\mathrm{T}}$$

$$u_2^* = [2.2747 \quad 0.2609]^{\mathrm{T}}.$$

Figure 3 illustrates that this solution is an ESS with two species. Each species' strategy satisfies the ESS maximum principle.

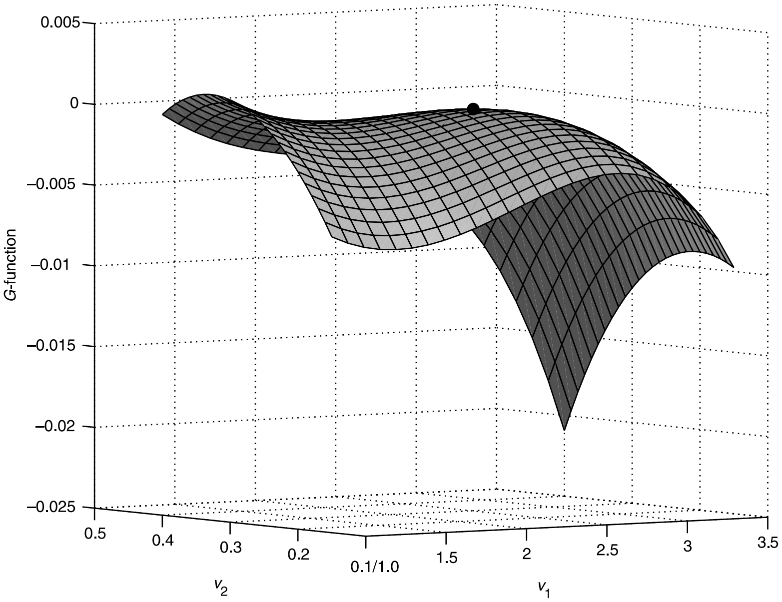

Fig. 2. Decreasing the prey's niche breadth from that of Fig. 1 changes the outcome. When the system is constrained to have a single species, then its strategy evolves to a peak that is just a local maximum, independent of its initial strategy value. This single species and its strategy are not an ESS.

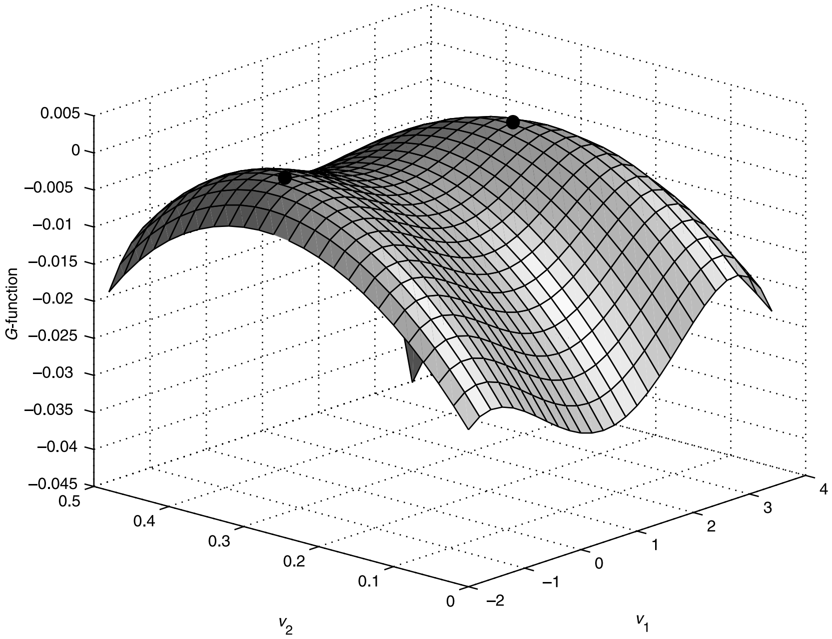

Fig. 3. Adaptive dynamics can produce an ESS for the model of Fig. 2, when the system starts with two or more species with sufficiently distinct initial strategy values. Not all starting conditions of species and their strategies will result in this ESS. For some starting conditions with two or more species, the system will converge on the single, local, non-ESS peak of Fig. 2.

Example 2 has two convergent-stable solutions. If we start the system with just a single species, it always evolves to the non-ESS local maximum shown in Fig. 2. If we start with two or more species, strategy values either continue to evolve towards the non-ESS solution of one species, or they evolve to the ESS of two species. The ESS is convergent stable locally but not globally. The strategy values of at least two of the initial species must be sufficiently far apart for the system to evolve to the ESS. It is noteworthy that the adaptive landscape at the ESS provides no insights or clues into the non-ESS convergent-stable solution, and the adaptive landscape at the non-ESS convergent-stable solution reveals little regarding the actual ESS. At the ESS, species 1 might be thought of as a competition avoider ($u_{11} < 0$) yet quite prone to engage in the tragedy of the commons ($u_{12} > 0$). Species 2 diverges to be a strong competitor ($u_{21} > 0$) and engages in the tragedy of the common ($u_{22} > 0$).

Example 3

We continue to consider larger values for σ_k, the variance term for carrying capacity. Let $\sigma_k = \sqrt{15}$. All other parameters retain their previous values. If we start with a single species, Darwinian dynamics evolve the strategy to a non-ESS convergent-stable saddle point as illustrated in Fig. 4. At this point, the first component of the strategy experiences disruptive selection (it is at a minimum) and the second component experiences stabilizing selection (it is at a maximum). We can permit adaptive speciation by introducing a new species at a strategy value close to the saddle point. With two species, the system evolves to an ESS of two species (Fig. 5).

With adaptive speciation it is easy for evolution by natural selection to evolve from the single-species convergent-stable saddle point to the ESS of two species. The two species' strategies will diverge from the saddle point no matter how close their starting values. This

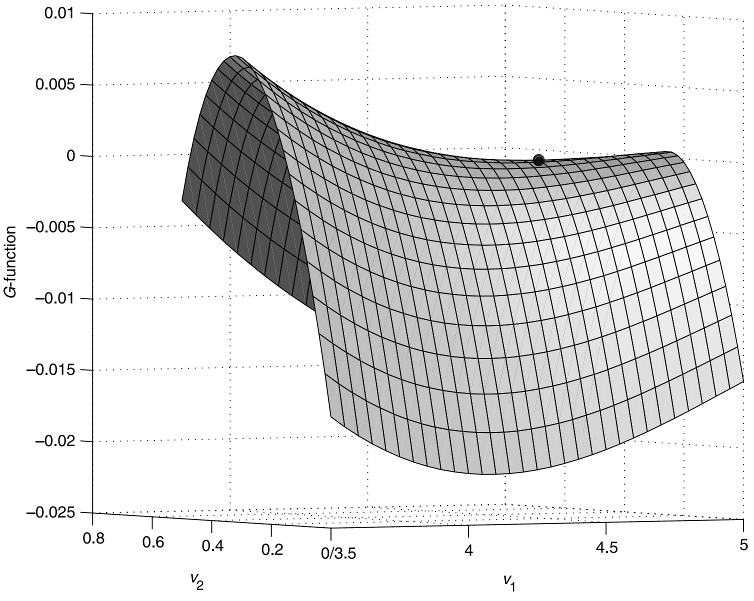

Fig. 4. A coalition of one results in a saddle point solution.

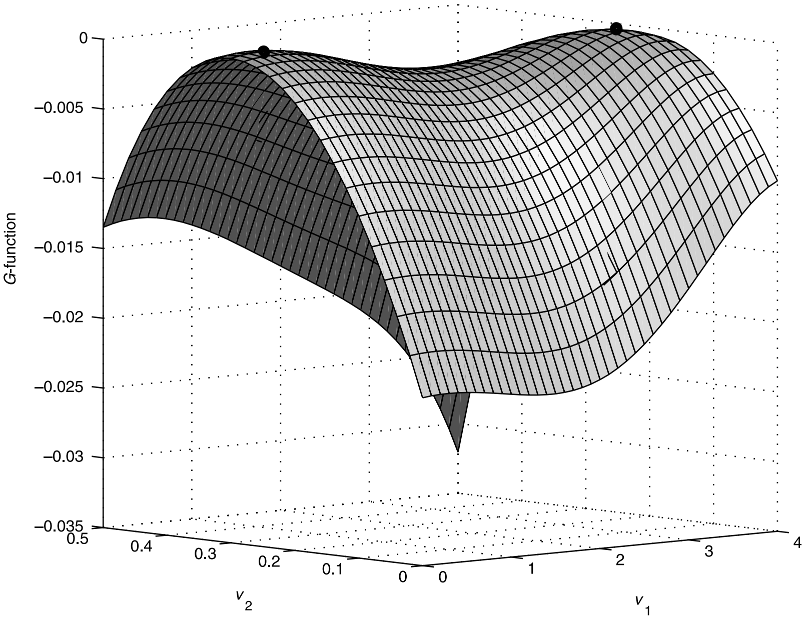

Fig. 5. Speciation allows for evolution to an ESS coalition of two.

speciation is being driven by the disruptive selection on the first strategy component. Nonetheless, two species that differ only with respect to their second components will still diverge as initial differences in the second component will drive co-adaptive changes in the first component.

Examples 2 and 3 contrast two environments, one with $\sigma_k = \sqrt{8}$ and the other with $\sigma_k = \sqrt{15}$. Both environments have an ESS with two species. And both environments have a convergent-stable solution that contains just one species, one at a local maximum and the other at a saddle point. Thus changes in a parameter can produce significant changes in the character of a non-ESS convergent-stable solution, yet produce no change in the character of the ESS. This behaviour was also found using scalar strategies (Cohen *et al.*, 1999).

Competition along two niche axes

We change the model by making carrying capacity, K, a bi-Gaussian function of the two components of a vector-valued strategy. This provides a vector-valued extension of the Lotka-Volterra model to include a two-dimensional niche axis. In this model, we let the second component of the strategy vector have similar effects on carrying capacity and competition as the first component. We let K take on a maximum when both strategy components are 0. We include a constant a that stretches or compresses the effect of the second strategy component on K. When $a > 1$, the second component, v_2, has a larger effect on K than the first strategy component, v_1. To measure competitive interactions, we simply sum the deviations in individuals' values for each of the strategy components. We use a parameter b to scale the effect of differences in $(v_2 - u_{j_2})$ relative to differences in $(v_1 - u_{j_1})$. When $b > 1$, deviations of individuals with respect to their second components will have larger effects on competition than deviations in their first strategy components. The model is given by

$$G(\mathbf{v},\mathbf{u},\mathbf{x}) = R\left(\frac{K(v) - \sum_{j=1}^{r}\alpha(\mathbf{v},\mathbf{u}_j)\,x_j}{K(\mathbf{v})}\right)$$

$$K = K_{\max}\exp\left(-\frac{v_1^2 + av_2^2}{2\sigma_k^2}\right)$$

$$\alpha(\mathbf{v},\mathbf{u}_j) = 1 + \exp\left[-\frac{((v_1 - u_{j_1}) + b(v_2 - u_{j_2}) + \beta)^2}{2\sigma_\alpha^2}\right] - \exp\left[-\frac{\beta^2}{2\sigma_\alpha^2}\right].$$

In the above, both carrying capacity and competition coefficients are bi-Gaussian functions of the two strategy components. Both strategy components can provide sources of stabilizing and disruptive selection. And both strategies can be expected to co-adapt. The value for one component should strongly influence the fitness-maximizing value for the other component. For instance, the structure of the competition coefficient encourages a co-adaptive positive covariance between v_1 and v_2. A negative covariance of these two components will tend to cancel out, whereas a positive covariance amplifies reductions in the competitive effects that an individual experiences from others.

Example 4

In this example we borrow most of the parameter values from Example 1, which produced an ESS with one species. Unlike Example 1, we no longer have the parameters associated with the tragedy of the commons and we now have the new parameters *a* and *b* that scale the effects of the second strategy component relative to the first. By setting $a = b = 1$, we have assumed that each strategy component has comparable effects on carrying capacity and competition:

$$N_x = 1$$

$$K_{\max} = 100$$

$$R = 0.25$$

$$\sigma_\alpha = 2$$

$$\sigma_k = \sqrt{2}$$

$$\beta = 2$$

$$a = 1$$

$$b = 1$$

Strategy dynamics result in the local maximum solution

$$x^* = 69.2202$$

$$u^* = [1.2131 \quad 1.2131].$$

Regardless of the starting conditions, Darwinian dynamics drive the system to the same local maximum when there is but a single species (Fig. 6). While the solution is convergent stable, it is not an ESS, as there are values for $\mathbf{v}$ that yield higher fitness than the convergent-stable point. Because the point is a maximum, the addition of a second strategy very close to this solution will not result in speciation. Both strategies will re-converge on the local maximum.

As in Example 2, to break away from this solution, an additional strategy must be located some distance away from the peak. In this case, the two species evolve to a new convergent-stable solution (Fig. 7):

$$\mathbf{x}^* = [66.3018 \quad 15.0239]$$

$$\mathbf{u}_1^* = [1.1333 \quad 1.1333]$$

$$\mathbf{u}_2^* = [-0.6415 \quad -0.6415].$$

These two strategies are distinct and form an ESS with two species. This ESS is only locally convergent stable. For some starting conditions on $\mathbf{u}_1$ and $\mathbf{u}_2$, the species converge on the single, non-ESS local maximum. For most starting conditions, the two species converge on the two-species ESS. For starting conditions with more than two species, $n_x > 2$, the community evolves either to the two-species ESS or to the single-species, non-ESS local maximum.

Had either the first or second strategy component been fixed at 0, the single-strategy evolutionary game would have resulted in a single-strategy ESS (Vincent *et al.*, 1993). The

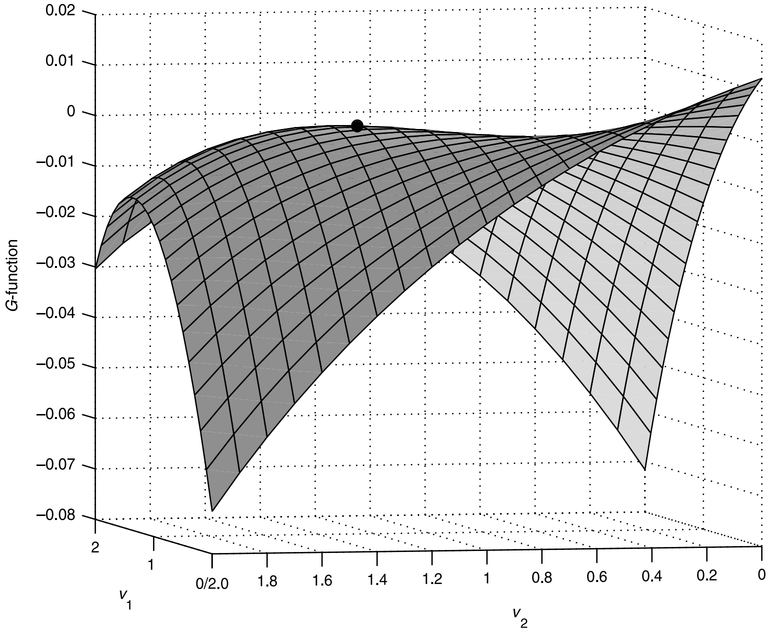

Fig. 6. With a single species, adaptive dynamics drives the species' strategy to a local maximum. While this strategy is not ESS, it is globally convergent stable when the system is constrained to have a single monomorphic species.

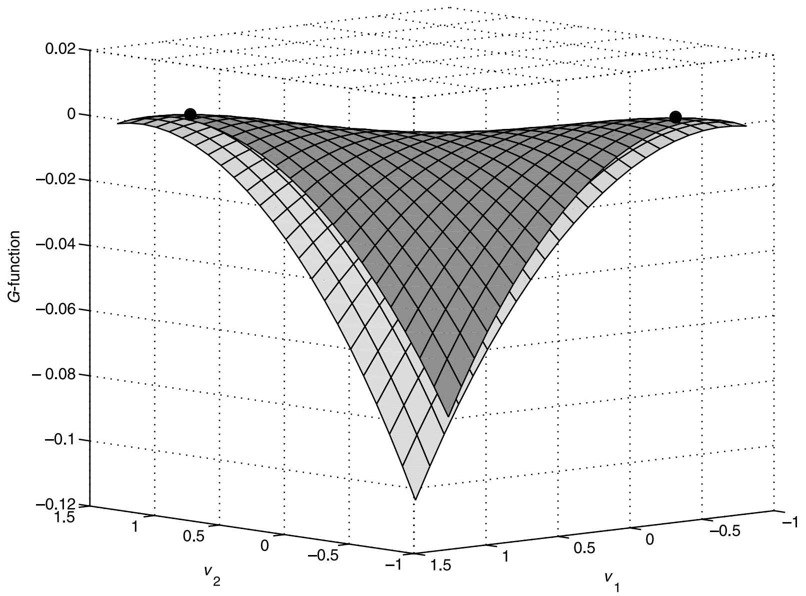

Fig. 7. An ESS coalition of two species for the same model as shown in Fig. 6. Adaptive dynamics results in an ESS, so long as the species' initial strategy values begin sufficiently far apart. For certain initial conditions, the two species' strategies converge on the same local maximum shown in Fig. 1.

addition of a second strategy and second dimension to the niche space increased species diversity at the ESS.

Example 5

In the final example, we change the parameters a and b so that the second strategy component no longer acts identically to the first. By making $a = 0.5$, carrying capacity is less sensitive to changes in v_2 than to changes in v_1. By making $b = 2$, competition is more sensitive to changes in v_2 than changes in v_1.

We start with a single species, $n_x = 1$. Regardless of the starting conditions on $\mathbf{u}_1$, Darwinian dynamics drive the system to the same saddle point (Fig. 8):

$$x^* = 19.1113$$

$$u^* = [1.2131 \quad 4.8515].$$

With just a single species, this saddle point is globally convergent stable. It represents a maximum on the landscape for the first strategy component and minimum for the second. The strategy is not ESS, and it is susceptible to invasion or to adaptive speciation.

We can simulate adaptive speciation by introducing a second species very close to the value of the first. Both of these species can have strategy values arbitrarily close to the saddle point solution. The strategy values of the two species diverge and evolution proceeds to a convergent-stable solution that preserves the two species (Fig. 9). The equilibrium solution to the left is an isolated peak and the equilibrium solution to the right is another saddle. While globally convergent stable with just two species, this two-species solution is not an ESS.

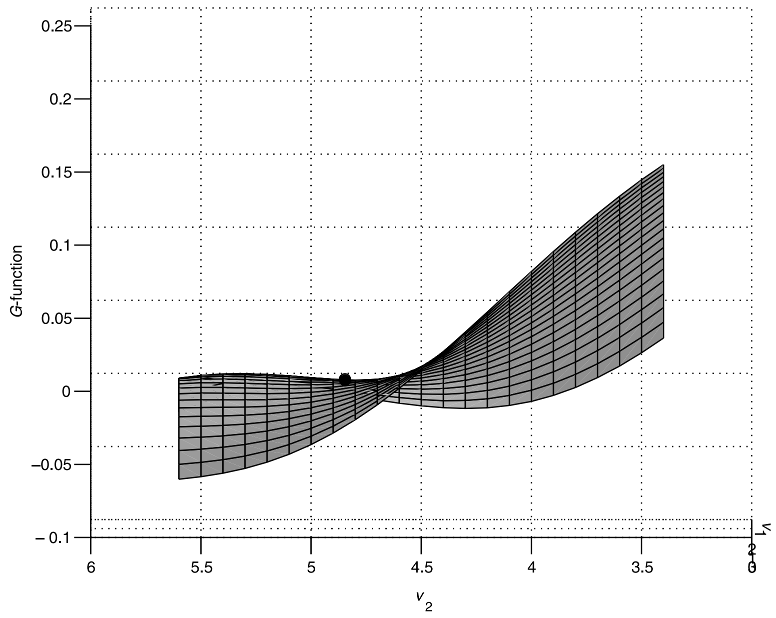

Fig. 8. A single species evolves to a convergent-stable saddle point. When constrained to have just one species, this saddle point is globally convergent stable and results independent of the species' initial strategy value.

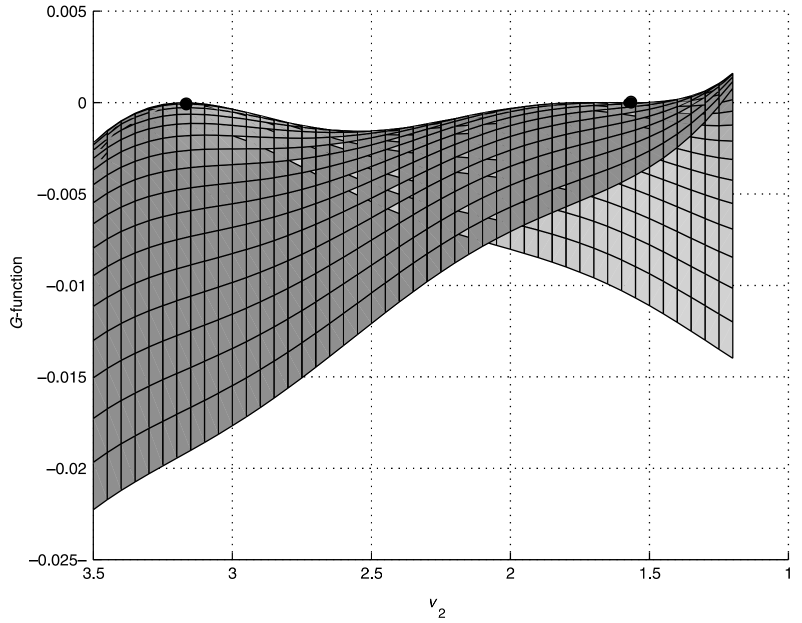

Fig. 9. Speciation of the single species of Fig. 8 and subsequent strategy dynamics of the two new species results in a convergent-stable system with one species at a peak and the other at a saddle. This is not yet an ESS.

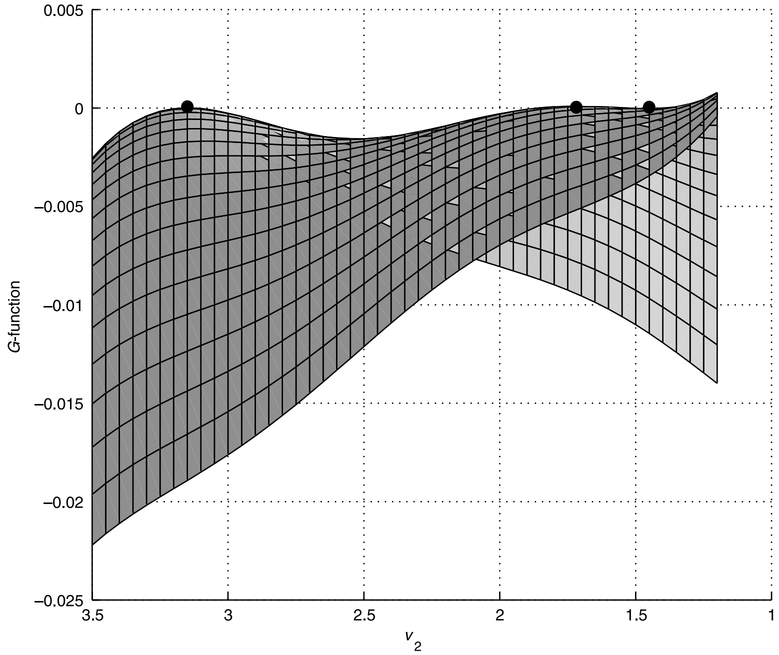

Fig. 10. Further speciation of the saddle point species of Fig. 9 and subsequent adaptive dynamics results in three species that evolve to a convergent-stable system with two species located at peaks and one at a saddle. This is not an ESS.

We can now let the species at the saddle point undergo adaptive speciation by keeping the first two species at their convergent-stable solutions and adding a new, rare strategy very near the saddle solution. They evolve to the two peaks and one saddle point as illustrated in Fig. 10. Finally, if we add one more mutant strategy near the saddle strategy of Fig. 10, one of them moves to the right-most peak of Fig. 11 and the other 'joins' the strategy previously occupying the peak to the left of the saddle in Fig. 10. The two co-evolved strategies now sit on top of the middle peak of Fig. 11. The three peaks in this figure correspond to an ESS coalition of three. This solution is only locally convergent stable on the ESS when the system has three or more species. When there are three or more species, the system always converges to one of the two three-species systems shown in Fig. 10 or Fig. 11. To get out of the non-ESS three-species system requires a fourth species that results either from invasion or speciation of the strategy at the saddle point.

Evolution by natural selection as an evolutionary game can sculpt the species' strategy values as well as the number of species. In this example, the second strategy component and its effects on carrying capacity and competition promote an ESS with three species. A single species will evolve to a saddle point where it is expected to undergo competitive speciation (Rosenzweig, 1978). The two-species system then evolves to a solution that has one species at a peak of the landscape and the other at a saddle point. Competitive speciation of this latter species creates a three-species community that co-evolves to the ESS.

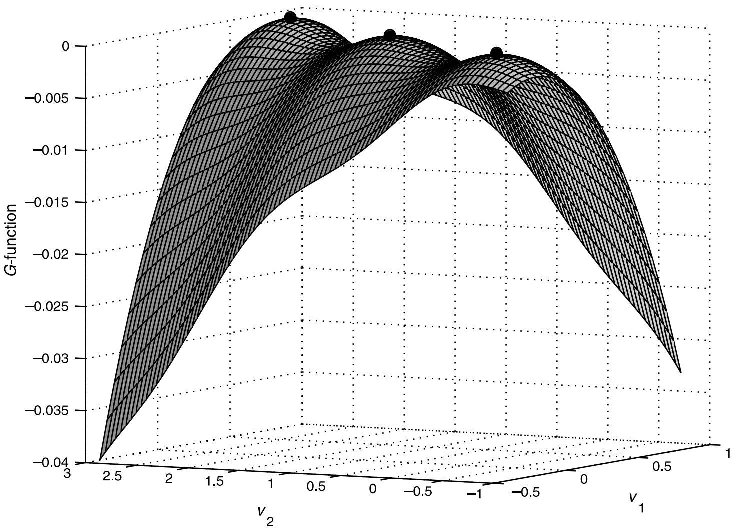

Fig. 11. Speciation of the species at the saddle point in Fig. 10 produces a four-species system. Adaptive dynamics acting on the four species results in two converging on the same peak, while the other two species converge on separate peaks. The resulting system is an ESS with a coalition of three distinct strategies and species.

PREDATOR–PREY

We can model predator–prey co-evolution by using two fitness-generating functions (Brown and Vincent, 1992): one *G*-function for the prey and one for the predators. The *G*-function of the prey extends the previous Lotka-Volterra model. The prey have a vector-valued strategy with two components. These components influence carrying capacity, competitive interactions, and the likelihood of being killed by the predator. We will give the predator a scalar-valued strategy. The predator's trait influence its likelihood of capturing prey.

We consider the following predator prey model:

$$\dot{x}_i = x_i\, G_x\,(\mathbf{v}, \mathbf{u}, \mathbf{w}, \mathbf{x}, \mathbf{y})|_{\mathbf{v}=\mathbf{u}_i}, \quad i = 1, \dots, s_x$$

$$\dot{y}_i = y_i\, G_y\,(\mathbf{v}, \mathbf{u}, \mathbf{w}, \mathbf{x}, \mathbf{y})|_{\mathbf{v}=\mathbf{u}_i}, \quad j = 1, \dots, s_y$$

where $\mathbf{x}$ denotes the prey and $\mathbf{y}$ the predators, and where $\mathbf{u} = [u_1, u_2]$ is the prey strategy and $\mathbf{w} = [w]$ is the scalar predator strategy. Both traits of $\mathbf{u}$ affect the carrying capacity additively, with a weighing ratio r_k that scales the effect of v_2 on K relative to the effect of v_1:

$$K(\mathbf{u}) = K_{\max} \exp\left\{-\frac{1}{2}\left[\left(\frac{v_1 - d_1}{\sigma_{k_1}}\right)^2 + r_k\left(\frac{v_2 - d_2}{\sigma_{k_2}}\right)^2\right]\right\}.$$

Carrying capacity takes on a global maximum when $(v_1, v_2) = (d_1, d_2)$.

Also, both traits of $\mathbf{u}$ affect competition additively with a weighing ratio r_α for the effect of v_2 relative to v_1:

$$\alpha(\mathbf{v}, \mathbf{u}) = 1 + \exp\left\{-\frac{1}{2}\left[\left(\frac{v_1 - u_1}{\sigma_{\alpha_1}}\right)^2 + r_\alpha\left(\frac{v_2 - u_2}{\sigma_{\alpha_2}}\right)^2\right]\right\}.$$

Unlike the previous examples, we have made competition symmetrical. And, competition is most intense between individuals that share the same strategy value.

We can model the interaction between the prey and the predator as:

$$\gamma(\mathbf{v}, \mathbf{w}) = a \exp\left\{-\frac{1}{2} v_2 \left[\frac{v_1 - w}{\sigma_\gamma}\right]^2\right\},$$

where γ is the rate at which a predator individual with strategy $\mathbf{w}$ captures prey with strategy $\mathbf{v}$. In this formulation, the prey's value for v_2 strongly influences what is adaptive for the prey and for the predator. If $v_2 > 0$, then the prey wants to have a value for v_1 that deviates from the predator's strategy, while the predator wants a strategy for w that matches v_1. Conversely, when $v_2 < 0$, then the prey wants its value for v_1 to match w, and the predator wants its value for w to deviate from v_1.

We can write the following G-functions for the prey and predator, respectively:

$$G_x = r_x \left[1 - \frac{\sum_{j=1}^{s_x} \alpha(\mathbf{v}, \mathbf{u}_j)\, x_j}{k(\mathbf{v})}\right] - \frac{\sum_{j=1}^{s_y} \gamma(\mathbf{v}, \mathbf{w}_j)\, y_j}{\sum_{j=1}^{s_x} x_j + b}$$

and

$$G_y = r_y \left[1 - \frac{\sum_{j=1}^{s_y} y_j}{c \sum_{j=1}^{s_x} \gamma(\mathbf{u}, \mathbf{v})\, x_j}\right].$$

The function γ gives the rate at which predators capture prey. As shown in the prey's G-function, the prey experience safety in numbers from the predators via a dilution effect. The greater the rate at which the predators consume prey, the closer their growth rate approaches a maximum given by r_y. Furthermore, via interference interactions, the population size of predators directly and negatively influences predator fitness.

The above model is a modified form of a Leslie predator–prey model with competition among the prey taking the form of Lotka-Volterra competition equations. While not necessarily a favoured form for predator–prey models, the Leslie model does have an important advantage for us. It possesses an explicit negative direct effect of predators on themselves. This produces positively sloped predator isoclines and increases the ease of obtaining stable population dynamics (as opposed to limit cycles).

We use the following parameter values:

$$\begin{aligned} &s_x = 2, \quad s_y = 1, \quad K = 100, \quad d_1 = d_2 = 1, \quad a = 0.15, \\ &r_k = r_\alpha = 0.5, \quad \sigma_{k_1} = \sigma_{k_2} = 4, \quad \sigma_{\alpha_1} = 4, \quad \sigma_{\alpha_2} = 2, \\ &b = 1, \quad c = 0.25, \quad r_x = r_y = 0.25. \end{aligned} \tag{2}$$

The ESS solution gives

$$\mathbf{x}^* = \begin{bmatrix} 1.0 \\ 1.0 \end{bmatrix}, \quad \mathbf{u}^* = \begin{bmatrix} 1.0 & 2.30 \\ 1.0 & -0.30 \end{bmatrix}, \quad y^* = 2.03, \quad w^* = 1.0$$

(see Figs. 12 and 13).

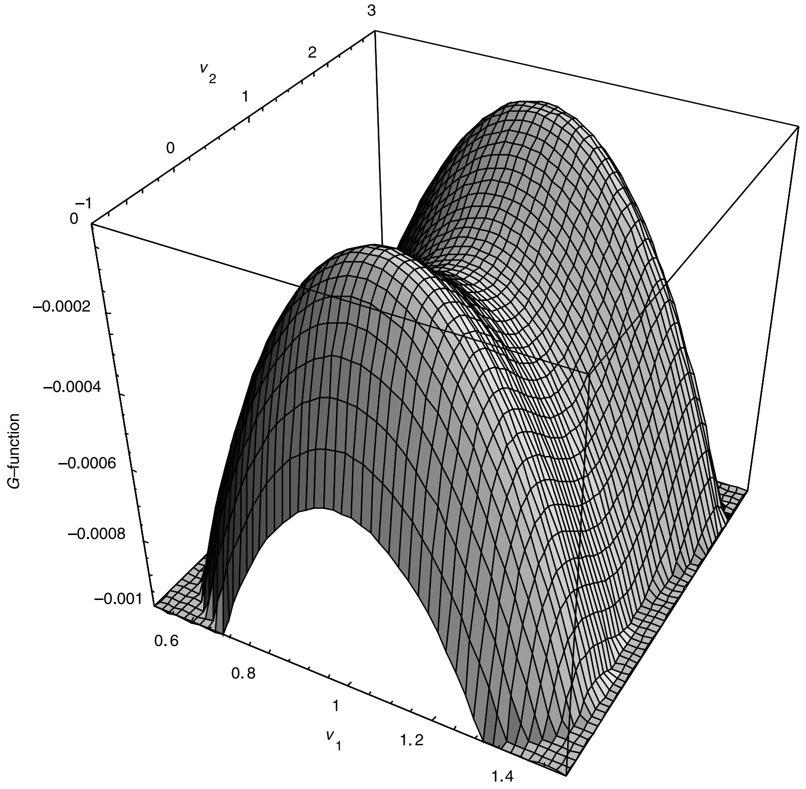

Fig. 12. Prey adaptive landscape at an ESS

Next, we use the same parameter values as in equation (2) with the following changes:

$$r_k = r_\alpha = 1, \quad s_x = 6, \quad \sigma_{\alpha_1} = 2, \quad \sigma_k = 5.$$

This results in the convergent-stable, but non-ESS, solution:

$$\mathbf{x} = \begin{bmatrix} 10.36 \\ 10.24 \\ 10.28 \\ 10.48 \\ 10.56 \\ 10.34 \end{bmatrix}, \quad \mathbf{u} = \begin{bmatrix} 1.930 & -0.300 \\ -0.074 & -0.242 \\ -1.129 & 1.060 \\ -0.050 & 2.297 \\ 2.166 & 2.252 \\ 3.122 & 1.000 \end{bmatrix}, \quad y = 2.23, \quad w = 1.0.$$

Figure 14 depicts the shape of the predator adaptive landscape at equilibrium. Note the local maximum at 1. Figure 15 shows the six prey species at a convergent-stable equilibrium. If we add more prey species (we added up to 10), they all simply settle to new positions around the crater's rim. If we add additional predator species in the neighbourhood of the current predator species, they simply converge on a single value that represents a local maximum of the predator's adaptive landscape. Neither the predator nor the prey is an ESS, each prey species occupies a convergent-stable saddle point. We did not investigate this

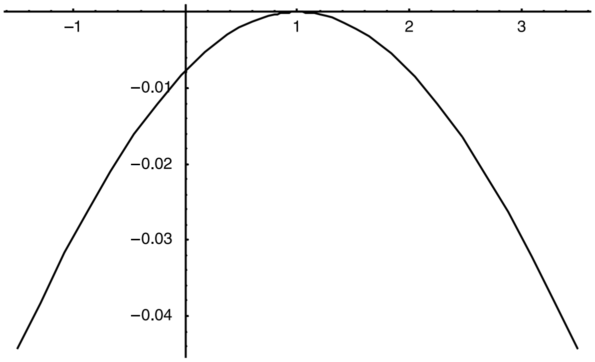

Fig. 13. Predator adaptive landscape at the ESS that contains a single prey and single predator species.

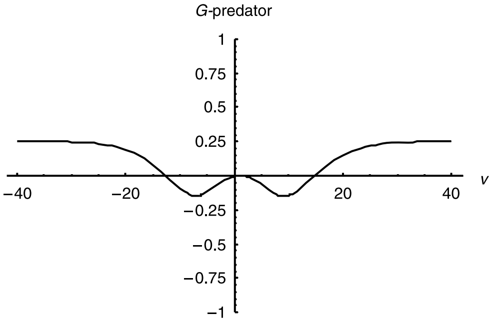

Fig. 14. Predator adaptive landscape when the strategy of the single predator species converges on a local maximum. At this point the system is not at an ESS. There are six prey species, each of which has converged on an evolutionarily stable saddle point; and there are predator strategies quite far from the predator's current strategy that would offer higher fitness to an individual predator in the current environment.

model further to determine whether this model has an ESS. The predators could possess additional co-existing species at evolutionary convergent stable points, if we began with several predator species with very different initial strategy values.

This particular predator–prey model can result in infinite niche packing for the prey (MacArthur and Levins, 1964, 1967; May, 1974). In the case where more than one prey species can converge on a circular rim of the adaptive landscape, any number of species can co-exist and be evolutionarily convergent stable. On the rim, each prey species converges on a saddle point. At this point, adaptive speciation can generate new prey species. These prey species diverge somewhat and come to occupy new positions on the rim that are also local saddle points. This process, in theory, could produce an infinite number of prey species occupying a continuum of niches around the rim. This provides an evolutionary-game exploration of a two-dimensional 'niche' space discribed in MacArthur and Levin's ecological model. Their model allowed for an infinite number of species to co-exist along a one-dimensional niche axis (May, 1974). In the evolutionary model, the niche axis does not exist except as a product of the interplay between ecological and evolutionary dynamics. Furthermore, the evolutionary

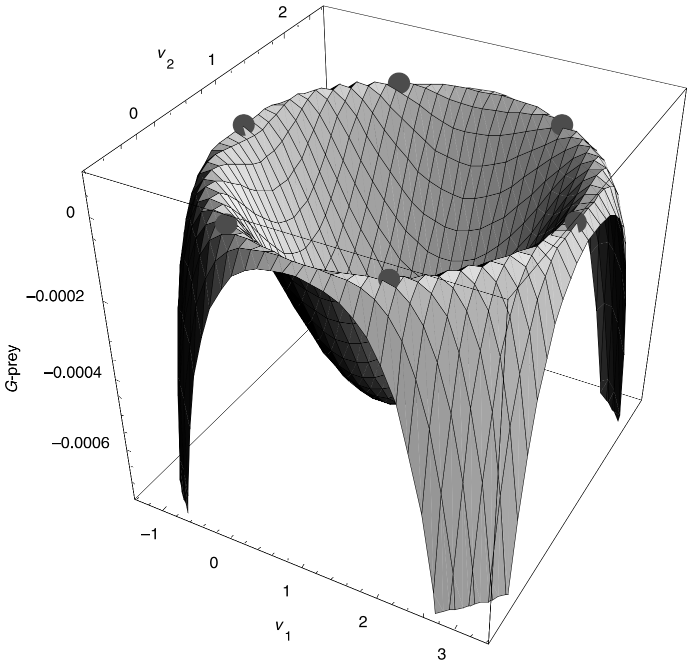

Fig. 15. Prey adaptive landscape at a convergent-stable equilibrium of six prey species. This is not an ESS. Each prey occupies a saddle point, and the predator strategy has converged on a local maximum only. With speciation, the additional prey species continue to occupy saddle points around the ever flatter crater.

dynamics stabilized at convergent-stable points regardless of whether these points were ESS. Other game theory models of predator–prey co-evolution have resulted in non-convergent adaptive dynamics (Marrow *et al.*, 1992; Rand *et al.*, 1994; Dieckmann *et al.*, 1995; Abrams and Harada, 1996).

DISCUSSION

Living organisms possess a suite of evolving characters. In evolutionary game theory, this suite of different heritable traits defines a vector-valued strategy. Each element of the vector describes the state of a particular trait. Vector-valued strategies expand the possibilities of using game theory to model frequency-dependent selection. Vector-valued strategies are more realistic, and they consider simultaneously the co-adaptation of different traits within the organism and the co-evolution of those traits between individuals and species. Vector-valued strategies pose two modelling challenges.

First, fitness must be formulated to include the effects of each trait, the trait values of others, the frequency of others in the population, and population size. The fitness function must determine both population dynamics and the dynamics on strategy frequencies. The fitness-generating function or *G*-function approach that we have used in the past always was applicable to vector-valued strategies (Vincent and Brown, 1988). In other words, the virtual strategy of the *G*-function may be a scalar (= single trait) or a vector (= several traits). This paper focuses on strategy dynamics of vector-valued strategies. The virtual strategy, $\mathbf{v}$, 'generates' the per capita growth rate of an individual possessing a particular strategy whether the strategy is present or not in the population. The virtual strategy can also be imagined as a very rare mutant or as the strategy of some arbitrary focal individual. The virtual strategy models unilateral changes in an individual's strategy while holding the strategies of the population constant. The other variables of the *G*-function give the current biotic environment, including the strategies of others in the population and the population size of each extant strategy in the population. In going from scalar-valued to vector-valued, the strategy of others, **u**, becomes a vector of vectors. The strategies of others includes the vector of strategy values currently found among individuals in the community, and each of these strategy values is also a vector of values for each trait within the strategy. Whether the strategy is scalar- or vector-valued, the vector of population sizes, **x**, remains the same: x_i gives the population size of individuals using strategy $\mathbf{u}_i$.

The definition of an ESS applies for both scalar- and vector-valued strategies (Vincent and Brown, 1988). An ESS must be resistant to invasion by rare alternative strategies. For this to be so, an ESS must satisfy the ESS maximum principle. The *G*-function must take on a maximum with respect to the virtual strategy when this strategy equals an ESS value and when the population is also at the ESS. In a biotic environment where others are at the ESS in regards to strategies and population sizes, an individual maximizes its own fitness by using a strategy of the ESS. Hence, the ESS is optimal in the sense that it maximizes *G* with respect to **v** (individual fitness). But an ESS will usually not be optimal in the sense of maximizing *G* with respect to the population's strategy, **u** (group fitness). In evolutionary game theory, the adaptive landscape is a plot of the *G*-function versus the virtual strategy. When the population is at an ESS, the strategies of the ESS are global maxima on this landscape. In going from scalar- to vector-valued strategies, the concepts of optimality remain the same. However, the adaptive landscape increases in dimensionality. The landscape surface has the same dimensionality as the strategy vector and it is plotted in a state space that has an axis for each trait of the strategy vector plus one additional axis for fitness.

An ESS must also be convergent stable. If strategy values are changed slightly from their ESS values, then Darwinian dynamics must return these values to the ESS. Darwinian dynamics includes changes in population size (population dynamics) and changes in the mean strategy value of each species (strategy dynamics). One goal of this paper is to present the proper expressions for strategy dynamics when strategies are vector-valued. We derive two expressions for how the mean value of a species' strategy will change with time. The first expression, given by equation (8) in the Appendix, shows how the gradients of the adaptive landscape along each of its component axes influence the rate of evolution of each trait value. The effect of a particular trait on its strategy dynamics is straightforward. The trait value will change in the direction of its slope on the adaptive landscape. And the rate of change will be proportional to the slope's magnitude. The trait value tends to 'climb' the adaptive landscape. However, the slopes of the landscape in the direction of other traits also influence a trait's direction and speed of evolution. This happens via any covariances among trait values within the strategy vector of the species. The rate of change in a trait's value includes the sum of these other slopes, weighting each slope by the covariance of the traits. This strategy dynamic combined with the population dynamics will bring convergence to an ESS (either locally or globally with respect to initial strategy values and population sizes).

More simply, strategy dynamics can be approximated by setting all of the covariance terms equal to zero as in equation (9) in the Appendix. In this case, a component of the strategy changes in the direction of the fitness gradient with respect to that component. And the rate of change will be proportional to the magnitude of the gradient. This dynamic is much simpler than considering the effects of any covariances among the traits. When are covariances among traits likely to be small? This question asks to what extent are the variances around the different trait values orthogonal. Natural selection, each time step, will promote some covariance structure as a result of co-adaptation between the different traits of the strategy. Within a species this should result in low covariances and especially so if the variances in trait values are relatively small. Furthermore, interbreeding among individuals within a species should make the distributions of values for each trait somewhat orthogonal.

When will the covariance terms be non-negligible? Large covariances are likely when traits are non-independent or when different traits experience partial linkage on the same chromosome. Non-independence can be incorporated into the *G*-function by specifying the functional relationships among the feasible trait values. In this way, the dimensionality of the strategy vector becomes reduced to the subset of effectively independent traits. When there are chromosomal linkages among trait values, co-adaptations can build up large covariances among the values of different traits, and these covariances break down proportionate to the rate of crossing over. In such a case, the strategy dynamics will proceed according to equation (8) with full consideration of the covariance terms. However, as the strategy approaches an ESS, the rate of change in trait values will slow down as the gradient becomes flat (at least for an ESS on the interior of the strategy set). However, the rate of recombination should remain the same as it is a property of the genetic system and not the adaptive landscape. Eventually recombination will reduce the covariance to the point where the traits associate independently as in (9). Note that conceptually traits do not necessarily represent a single gene, and they may be dependent. These dependencies result in manifolds in the trait space, and it is these manifolds that we use as traits to preserve heritable independence among traits.

The Darwinian dynamics include both population dynamics (changes in $\mathbf{x}$) and strategy dynamics (changes in $\mathbf{u}$). The fitness-generating function describes the former and the gradients of the *G*-function influence the latter dynamics. Beginning with a fixed number of species, the evolutionary dynamics may converge on particular strategy values. These solutions are convergent stable. The number of different strategies at the convergent-stable point may be equal to or less than the starting number of species. It will be less than the number of strategies when two or more species converge on the same strategy value. The convergent-stable point may represent peaks on the adaptive landscape that are global as well as local maxima. If so, the point conforms to the ESS maximum principle, and it is an ESS. The convergent-stable point may represent peaks on the landscape, but the peaks may be local and not global. In such a case, the convergent-stable point is not resistant to invasion, and it is not an ESS. Darwinian dynamics alone cannot escape from the local maxima to strategy values that yield higher fitness. To add species and achieve the ESS requires the invasion of novel strategies that are quite distant from the strategy values of the extant species (Cohen *et al.*, 1999).

The convergent-stable point under vector-valued strategies may be a saddle point of the adaptive landscape. This situation is analogous to the evolutionarily stable minimum of systems with scalar-valued strategies (Brown and Pavlovic, 1992; Abrams *et al.*, 1993b). At the saddle point, the value of at least one of the traits represents a minima along the trait's axis. Competitive speciation (Rosenzweig, 1978; Cohen *et al.*, 1999; Mitchell, 2000) can produce a daughter species. Convergent-stable saddle points often occur when the number of species in the co-evolving community falls below the number required for the ESS. For instance, a community ESS may include three species. With just a single species, evolutionary dynamics may converge on a saddle point. Speciation now increases the number of species to two. The co-evolution of these two species may converge on a set of points where one occupies a local, but not global, maximum and the other occupies another saddle point. Speciation at the saddle point increases the community to three species. These three species likely co-evolve and converge on the ESS. As in the scalar-valued case (Metz *et al.*, 1996; Geritz *et al.*, 1998; Geritz, 1998; Cohen *et al.*, 1999), adaptive dynamics of a vector-valued strategy can influence both the number of species and their strategy values. Empirical evidence is mounting to suggest that this sort of speciation may occur in systems including apple maggot flies (Feder *et al.*, 1988), bacteria (Lenski *et al.*, 1991; Lenski and Travisano, 1994), fruit flies (Rice and Salt, 1990; Rice and Hostert, 1993), and sticklebacks (Schluter, 1994).

Vector-valued strategies add complexity to natural selection. A single species with a scalar-valued strategy only experiences selection from the predominant strategy of the species. Several species with scalar-valued strategies experience co-evolution. The strategy dynamics of each species can be influenced by each of the species' strategy values. The strategy values of the different species at the ESS will reflect these co-evolutionary effects. A single species with a scalar-valued strategy experiences co-adaptation among the different traits comprising the strategy. The ESS value of a given trait, v_i, will reflect the effects of the individual's other traits, v_j, as well as the values for each trait in the species at large, u_k. For a strategy with three traits, the strategy dynamics of the first trait will be influenced by five other trait values (two others within the individual and the three comprising the strategy of the species). Several species with vector-valued strategies experience both co-adaptation among the trait values within a strategy and co-evolution among the trait values across species. The ESS value for a given trait within a given species will reflect the effects of the individual's other traits, the values for each trait of its species, and the trait values of the other species. We suggest reserving the term 'co-evolution' to describe evolutionary effects of strategy values between species and the term 'co-adaptation' to describe evolutionary effects of traits on each other within the strategy of the individual. Co-evolution occurs among species. Co-adaptation occurs within an individual.

The adaptive landscape represents a plot of the fitness-generating function versus the strategy of the individual. It is a plot of G versus $\mathbf{v}$ where the strategies of the population, $\mathbf{u}$, and their abundances, $\mathbf{x}$, are held fixed. With vector-valued strategies, the adaptive landscape is multi-dimensional. If the strategy comprises two traits, the landscape will be a surface, with three traits a volume, etc. Strategy dynamics occur in response to the species' current position on the fitness gradients of the landscape. Strategy dynamics occur in response to $\partial G/\partial \mathbf{v}$. The landscape is also useful for evaluating whether a convergent-stable solution to the strategy dynamics is a maximum or minimum, or whether it as an ESS. The current landscape not only determines strategy dynamics, but the resultant changes in strategy values among and within species will change the shape of the landscape. The landscape is flexible to changes in $\mathbf{u}$. With frequency-dependence, the landscape can be likened to one or more people traversing a waterbed. With each step (or movement of a species' strategy) the waterbed's surface, like the adaptive landscape, can rise and fall. Evolutionary movement by evolving species results in the shifting, creation, and disappearance of topological features such as peaks, valleys, and ridges. The flexibility of the landscape with strategy dynamics is described by the magnitude of the effect of changing the species strategy on the fitness gradients of the landscape. Thus, flexibility is defined by the magnitudes of $\partial^2 G/\partial \mathbf{v}\partial \mathbf{u}$. When the effect of **u** on the fitness gradient is zero, then the landscape is rigid, when it is large, the landscape changes rapidly with strategy dynamics.

With multi-dimensional strategies and landscapes, the opportunities for flexibility of the landscape increases. With a single trait, there is just one factor offering possibilities for flexibility and that term is $\partial^2 G/\partial v_1 \partial u_1$. With two traits, there are four avenues for flexibility represented by all combinations of $i = 1, 2$ and $j = 1, 2$ in the terms $\partial^2 G/\partial v_i \partial u_j$. With three traits, there are nine avenues for flexibility, etc. It is the possibility for frequency-dependent selection, the characterization of the *G*-function, and these avenues for flexibility in the landscape's shape with strategy dynamics that distinguish the adaptive function of *G* versus **v** from the more familiar Wrightian landscape of *W* versus **p**, where *W* is a measure of population fitness as a function of the vector of gene frequencies at each loci, **p** (Wright, 1931, 1960, 1969; Wade, 1996; Wade and Goodnight, 1998). It is the rigidity of the Wrightian landscape and the lack of distinction between the effects of the individual's strategy, **v**, from the effects of changing the population's strategy, **u**, that has obscured an appreciation for the interplay between strategy dynamics, $\partial G/\partial \mathbf{v}$, and landscape dynamics, $\partial^2 G/\partial \mathbf{v}\partial \mathbf{u}$, for evolution, co-adaptation, co-evolution, and speciation.

There are several examples in the literature that model evolutionary games with vector-valued strategies. Rosenzweig (1978) and Brown (1990, 1996) consider the co-adaptation of the behavioural trait of diet selectivity with a fixed morphological trait influencing diet specialization. The ESSs may include one or several species that have different degrees of diet pickiness and morphological specializations. As a general rule, morphological specialists tend to be more behaviourally selective and generalists tend to be more opportunistic. These works did not use strategy dynamics or the multi-dimensional landscapes to characterize and find the ESSs. Model analysis was simplified by assuming that the behavioural trait could change much more rapidly than the morphological trait. Thus, an individual was assumed to acclimate behaviourally to its morphology by selecting its fitness-maximizing behaviour given its morphology and the current ecological circumstances. In this way, the ESS was solved in a two-step manner. Conditions were found for the optimal behaviour given set morphologies, and then the ESS morphology was found assuming that the behaviour changed instantly and accordingly. This aspect of rapid behavioural adjustments and slower morphological adjustments can be considered using adaptive dynamics by assuming that the speed coefficient governing strategy dynamics is much larger for the behavioural than for the morphological traits. In fact, any hierarchy with respect to evolutionary rates among traits within a vector-valued strategy can be accommodated by appropriate adjustments of these rate coefficients.

The strategy dynamics for vector-valued strategies is similar to the evolution of quantitative traits in quantitative genetic models (Charlesworth, 1990). In quantitative genetics models, the change in values of a suite of quantitative traits is proportional to the fitness gradients multiplied by the matrix of genetic or phenotypic covariances (Cheverud, 1988). The fitness function, *W*, becomes like a *G*-function when natural selection is frequency-dependent. The *W*-function of quantitative genetics includes a term for a 'mutant' value of the trait (like the virtual strategy of evolutionary game theory) and the current values for the quantitative traits within the population. In quantitative genetics models, the fitness gradient considers the change in *W* with a change in the mutant, evaluated at the population's current values for the traits. The phenotypic covariance matrix of quantitative genetics is analogous to the matrix of covariances among the components of the strategy. In quantitative genetics, these covariance terms are often fixed under the assumption that they represent developmental, linkage or genetic constraints (Lande, 1979; Arnold and Wade, 1984). In general, however, the covariance terms vary considerably among related species (Steppan, 1997a, 1997b), and these terms probably change rapidly with time and selection (Lofsvold, 1986). As in the case of the evolutionary games, the appropriate *G*-matrix describes the covariances among traits within a population, and not covariances of traits among related species or populations. Both the evolutionary dynamics of game theory and the dynamics of quantitative genetics extend Fisher's fundamental theorem of natural selection (Fisher, 1958) to consider vectors of traits and frequency-dependent selection. The appropriate formulation of the fitness gradient describes the direction and magnitude of evolutionary change, the covariance matrix incorporates any non-independencies, constraints or co-adaptations among traits of the strategy, and the additive genetic variance of Fisher becomes a speed term that scales the rate of evolutionary change.

Evolutionary game theory and adaptive dynamics have been applied to strategies that contain just a single trait (Abrams *et al.*, 1993a; Vincent *et al.*, 1993; Metz *et al.*, 1996). Here we extend the theory of adaptive dynamics to strategies that are multidimensional and consist of more than one trait. Three related tools greatly facilitate understanding the outcomes of the evolution of vector-valued strategies: strategy dynamics, the ESS maximum principle, and adaptive landscapes. With these tools it is possible to evaluate solutions for convergence stability and resistance to invasion, both properties of an ESS. Willis *et al.* (1991) asked, 'Can one predict the evolution of quantitative characteristics without genetics?' For both scalar- and vector-valued strategies, we believe the answer is 'yes'. Furthermore, explicit genetic knowledge or assumptions can be built directly into the evolutionary game to evaluate their effects on strategy dynamics (Hammerstein, 1996; Kisdi and Geritz, 1999). With the present state of evolutionary game theory, it is possible to model: (1) evolution among very distinct groups of species using different *G*-functions for each species group [e.g. predator–prey co-evolution (Brown and Vincent, 1992); (2) evolution among the different evolving species or populations within a *G*-function that has a multi-strategy ESS (e.g. co-evolution among closely related competitors); (3) co-adaptation and simultaneous evolution of all of the traits of interest within an individual (vector-valued strategies).

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APPENDIX: DERIVATION OF ADAPTIVE DYNAMICS FOR VECTOR-VALUED STRATEGIES

For each species i there are n_p phenotypes. We assume that the n_p phenotypes within a species mate assortatively (like mates with like). In general, the variability in strategy values within $\mathbf{u}_i$ will be small relative to the strategy differences among the different $\mathbf{u}_i$'s. Using triple subscripts, the difference between a nominal mean values and the actual strategy values of all extant phenotypes within species i can be represented by the matrix

$$\delta\mathbf{U}_i = \begin{bmatrix} \delta u_{i11} & \delta u_{i12} & \dots & \delta u_{i1n_p} \\ \delta u_{i21} & \delta u_{i22} & \dots & \delta u_{i2n_p} \\ \vdots & \delta u_{ijk} & \ddots & \vdots \\ \delta u_{in_u1} & \delta u_{in_u2} & \dots & \delta u_{in_un_p} \end{bmatrix},$$

where each row represents the variations in a given component of the strategy vector and each column represents a *phenotype*. At $t = 0$, u_i can take on any value drawn from the strategy set. The first subscript represents the different species i. The second represents the trait within a strategy; there are n_u such traits. The third subscript represents the phenotype. There are n_p phenotypes, and each column represents the set of traits that a phenotype carries. A unique set of traits represents a phenotype's strategy. Note that δ is not a variable, but δu_{ijk} is. The latter can be viewed as representing all possible values of a trait.

In terms of this notation, the set of strategies represented by all the phenotypes is given by

$$\mathbf{U}_i = \begin{bmatrix} u_{i1} + \delta u_{i11} & u_{i1} + \delta u_{i12} & \dots & u_{i1} + \delta u_{i1n_p} \\ u_{i2} + \delta u_{i21} & u_{i2} + \delta u_{i22} & \dots & u_{i2} + \delta u_{i2n_p} \\ \vdots & u_{ij} + \delta u_{ijk} & \ddots & \vdots \\ u_{in_u} + \delta u_{in_u1} & u_{in_u} + \delta u_{in_u2} & \dots & u_{in_u} + \delta u_{in_un_p} \end{bmatrix}$$

which may be written more conveniently as

$$\mathbf{U}_i = \mathbf{u}_i\Omega + \delta\mathbf{U}_i,$$

where

$$\Omega = [1 \quad 1 \cdots 1]$$

is a row vector containing n_p ones. Thus, $\mathbf{u}_i\Omega$ is an $n_u \times n_p$ matrix, and to it is added, term by term, the deviation of phenotype trait values from the species mean $\mathbf{u}_i$. Note that under this matrix notation, the changes in the components of u_{ij} are independent, since the components of δu_{ij} are independent. While such genetic phenomena such as linkage, epistasis, and pleiotropy may force dependencies among the components of the strategy vector, we assume here that such phenomena do not preclude the components from varying independently of each other. By making this assumption, any subsequent covariances in the components' strategy dynamics and among the values of components is due to adaptive dynamics and co-adaptation, not forced genetic or physical constraints on the strategy set.

It is possible that some of the phenotypes differ from the mean strategy vector in only one component of the mean strategy vector. The density of phenotypes within the population using these strategies is designated by x_{ij}. Thus the density of the species x_i may be written as the sum of the densities of all the phenotypes within species i:

$$x_i = \sum_{j=1}^{n_p} x_{ij}. \tag{3}$$

The mean strategy for population x_i is defined as

$$\mathbf{u}_i = \sum_{j=1}^{n_p} \frac{x_{ij}}{x_i} \mathbf{u}_{ij}, \tag{4}$$

where $\mathbf{u}_{ij}$ is the jth column vector of $\mathbf{U}_i$.

We can track how the mean strategy $\mathbf{u}_i$ evolves (i.e. a strategy dynamic for $\mathbf{u}_i$) by simply considering the changes that must take place in the mean strategy as a result of changes in phenotype densities within population i. If we define

$$q_{ij} = \frac{x_{ij}}{x_i}$$

and

$$\mathbf{q}_i = [q_{i1} \cdots q_{in_p}]^{\mathrm{T}},$$

then (4) may be written in the following compact matrix form:

$$\mathbf{u}_i = \mathbf{U}_i \mathbf{q}_i. \tag{5}$$

We may now calculate a strategy dynamic for the mean strategy $\mathbf{u}_i$ using (5). Here we use the idea that the dynamics of $\mathbf{u}_i$ as it changes from its original nominal value are due to changes in the relative frequency of phenotypes (the q_{ij}). Even though $\mathbf{u}_i$ changes with time, we may take $\mathbf{U}_i$ constant since n_p can be a very large number with only a fraction of the possible phenotypes having a non-zero q_{ij} at any point in time. A cluster of non-zero and ever-changing q_{ij} phenotype strategies is able to follow $\mathbf{u}_i$ as a distribution of strategies about the mean. In other words, the change in $\mathbf{u}_i$ is due to a change in $\mathbf{q}_i$ only as given by

$$\dot{\mathbf{u}}_i = \mathbf{U}_i \dot{\mathbf{q}}_i.$$

In terms of the *G*-function, the population dynamics for the species and the phenotypes are written as

$$\begin{aligned} \dot{x}_i &= G|_{\mathbf{u}_i} x_i \\ \dot{x}_{ij} &= G|_{\mathbf{u}_{ij}} x_{ij}. \end{aligned} \tag{6}$$

It follows that

$$\dot{q}_{ij} = \frac{x_i \dot{x}_{ij} - x_{ij} \dot{x}_i}{x_i^2} = \frac{x_i x_{ij}\, G|_{\mathbf{u}_{ij}} - x_{ij} x_i\, G|_{\mathbf{u}_i}}{x_i^2} = q_{ij}\left(G|_{\mathbf{u}_{ij}} - G|_{\mathbf{u}_i} \right),$$

which may be written in matrix form as

$$\dot{\mathbf{q}}_i = \mathbf{Q}_i \Delta \mathbf{G}_i,$$

where $\mathbf{Q}_i$ is a diagonal matrix with $q_{i1}, q_{i2}, \ldots, q_{in_p}$ down the diagonal:

$$\Delta \mathbf{G}_i = \begin{bmatrix} G|_{\mathbf{u}_{i1}} - G|_{\mathbf{u}_i} \\ \vdots \\ G|_{\mathbf{u}_{in_p}} - G|_{\mathbf{u}_i} \end{bmatrix}.$$

Thus the strategy dynamic may be written as

$$\dot{\mathbf{u}}_i = \mathbf{U}_i \mathbf{Q}_i \Delta \mathbf{G}_i. \tag{7}$$

Note that a minimal set of assumptions has been used to obtain (7), namely that there exists a finite number of fixed strategies available to the phenotypes. This result may be used ‘as is’ to determine the strategy dynamics. However, this requires keeping track of perhaps large numbers of phenotypes, and one may need to know the form of distribution of strategies around the mean strategy. A reasonable assumption assigns the majority of the population to phenotypes within the immediate neighbourhood of the mean strategy.

However, all phenotypes must occur as some fraction of the population, even though this fraction might be quite small or even zero.

We now use a Taylor series expansion to approximate $\mathbf{\Delta G}_i$ in terms of first-order and higher-order terms (HOT):

$$\begin{bmatrix} G|_{\mathbf{u}_{i1}} - G|_{\mathbf{u}_i} \\ \vdots \\ G|_{\mathbf{u}_{in_p}} - G|_{\mathbf{u}_i} \end{bmatrix} = \begin{bmatrix} \frac{\partial G}{\partial v_1}\Big|_{\mathbf{u}_i} \delta u_{i11} + \frac{\partial G}{\partial v_2}\Big|_{\mathbf{u}_i} \delta u_{i21} + \ldots + \frac{\partial G}{\partial v_{n_u}}\Big|_{\mathbf{u}_i} \delta u_{in_u1} \\ \vdots \\ \frac{\partial G}{\partial v_1}\Big|_{\mathbf{u}_i} \delta u_{i1n_p} + \frac{\partial G}{\partial v_2}\Big|_{\mathbf{u}_i} \delta u_{i2n_p} + \ldots + \frac{\partial G}{\partial v_{n_u}}\Big|_{\mathbf{u}_i} \delta u_{in_un_p} \end{bmatrix} + \text{HOT}$$

$$= \begin{bmatrix} \delta u_{i11} & \delta u_{i21} & \ldots & \delta u_{in_u1} \\ \delta u_{i12} & \delta u_{i22} & \ldots & \delta u_{in_u2} \\ \vdots & \vdots & \ddots & \vdots \\ \delta u_{i1n_p} & \delta u_{i2n_p} & \ldots & \delta u_{in_un_p} \end{bmatrix} \begin{bmatrix} \frac{\partial G}{\partial v_1} \\ \frac{\partial G}{\partial v_2} \\ \vdots \\ \frac{\partial G}{\partial v_{n_u}} \end{bmatrix}_{\mathbf{u}_i} + \text{HOT}$$

For small $\delta \mathbf{u}_{ij}$ this gives:

$$\mathbf{\Delta G}_i \simeq \delta \mathbf{U}_i^{\mathrm{T}} \frac{\partial G}{\partial \mathbf{v}}\Big|_{\mathbf{u}_i}.$$

If we treat this equation as an equality and substitute it into (7), we obtain:

$$\begin{aligned} \dot{\mathbf{u}}_i &= \mathbf{U}_i \mathbf{Q}_i \delta \mathbf{U}_i^{\mathrm{T}} \frac{\partial G}{\partial \mathbf{v}}\Big|_{\mathbf{u}_i} \\ &= [\mathbf{u}_i \mathbf{\Omega} + \delta \mathbf{U}_i]\, \mathbf{Q}_i \delta \mathbf{U}_i^{\mathrm{T}} \frac{\partial G}{\partial \mathbf{v}}\Big|_{\mathbf{u}_i} \\ &= (\mathbf{u}_i \Omega \mathbf{Q}_i \delta \mathbf{U}_i^{\mathrm{T}} + \delta \mathbf{U}_i \mathbf{Q}_i \delta \mathbf{U}_i^{\mathrm{T}}) \frac{\partial G}{\partial \mathbf{v}}\Big|_{\mathbf{u}_i}. \end{aligned}$$

If we assume that q_{ij} and $\delta \mathbf{u}_{ij}$ are symmetric, we can now show that the first term is zero, i.e.

$$\mathbf{u}_i \Omega \mathbf{Q}_i \delta \mathbf{U}_i^{\mathrm{T}} = \mathbf{0},$$

since

$$\begin{bmatrix} u_{i1} & u_{i1} & \ldots & u_{i1} \\ u_{i2} & u_{i2} & \ldots & u_{i2} \\ \vdots & \vdots & \vdots & \vdots \\ u_{in_u} & u_{in_u} & \ldots & u_{in_u} \end{bmatrix} \begin{bmatrix} q_{i1} & 0 & \ldots & 0 \\ 0 & q_{i2} & \ldots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \ldots & q_{in_u} \end{bmatrix} \begin{bmatrix} \delta u_{i11} & \delta u_{i21} & \ldots & \delta u_{in_u1} \\ \delta u_{i12} & \delta u_{i22} & \ldots & \delta u_{in_u2} \\ \vdots & \vdots & \ddots & \vdots \\ \delta u_{i1n_p} & \delta u_{i2n_p} & \ldots & \delta u_{in_un_p} \end{bmatrix}$$

$$= \begin{bmatrix} u_{i1}q_{i1} & u_{i1}q_{i2} & \ldots & u_{i1}q_{in_u} \\ u_{i2}q_{i1} & u_{i2}q_{i2} & \ldots & u_{i2}q_{in_u} \\ \vdots & \vdots & \vdots & \vdots \\ u_{in_uq_i1} & u_{in_uq_i2} & \ldots & u_{in_uq_{in}\mathrm{u}} \end{bmatrix} \begin{bmatrix} \delta u_{i11} & \delta u_{i21} & \ldots & \delta u_{in_u1} \\ \delta u_{i12} & \delta u_{i22} & \ldots & \delta u_{in_u2} \\ \vdots & \vdots & \ddots & \vdots \\ \delta u_{i1n_p} & \delta u_{i2n_p} & \ldots & \delta u_{in_u\mathrm{n}_p} \end{bmatrix}.$$

Multiplying this result yields a matrix

$$\begin{bmatrix} u_{i1}\,(q_{i1}\delta u_{i_{11}} + q_{i2}\delta u_{i12} + \ldots + q_{in_u}\,\delta u_{i1n_p}) & \ldots & u_{i1}\,(q_{i1}\delta u_{in_u1} + q_{i2}\delta u_{in_u2} + \ldots + q_{in_u}\delta u_{in_un_p}) \\ \vdots & \vdots & \vdots \\ u_{in_u}\,(q_{i1}\delta u_{i_{11}} + q_{i2}\delta u_{i12} + \ldots + q_{in_u}\,\delta u_{i1n_p}) & \ldots & u_{in_u}\,(q_{i1}\delta u_{in_u1} + q_{i2}\delta u_{in_u2} + \ldots + q_{in_u}\delta u_{in_un_p}) \end{bmatrix}$$

in which each term sums up to zero due to the assumed symmetry. This leaves us with the result

$$\dot{\mathbf{u}}_i = \delta\mathbf{U}_i\mathbf{Q}_i\delta\mathbf{U}_i^{\mathrm{T}}\frac{\partial G}{\partial\mathbf{v}}\bigg|_{\mathbf{u}_i}.$$

Finally, if we define the covariance matrix

$$\mathfrak{D}_i = \delta\mathbf{U}_i\mathbf{Q}_i\delta\mathbf{U}_i^{\mathrm{T}}$$

we obtain the result

$$\dot{\mathbf{u}}_i = \mathfrak{D}_i\,\frac{\partial G}{\partial\mathbf{v}}\bigg|_{\mathbf{u}_i}. \tag{8}$$

Because of interbreeding and heritable independence among the strategy components, the off diagonal components will be small and made even smaller by the summation of both positive and negative terms. If the off diagonal terms are close to zero relative to the diagonal terms, we may write the strategy dynamics for each phenotype of the species i as

$$\dot{u}_{ik} = \sigma_{ik}\,\frac{\partial G}{\partial v_k}\bigg|_{\mathbf{u}_i}, \tag{9}$$

where σ_{ik} is the diagonal element corresponding to phenotype k.