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G-functions for the hermeneutic circle of evolution

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Abstract

Evolution by natural selection may include both frequency and density-dependence. Frequency-dependent selection is a kind of hermeneutic circle. As a literary term (and a school of philosophy), a hermeneutic circle describes how each word of a sentence or paragraph simultaneously draws its meaning from its context (the other words) and contributes towards the context. Frequency dependence is like this. Under frequency dependence, the fitness of an individual is not only influenced by its own heritable phenotype (in evolutionary game theory heritable phenotype = strategy) but by the frequency of strategies found among others in the population. And, the fitness accrued by individuals with a particular strategy will in time influence the frequency of strategies in the population. The challenge is to develop conceptual and modeling tools that allow us to determine the outcome of this hermeneutic circle of evolution. We need a fitness concept that defines the fitness of (or payoff to) individuals as influenced by both their own strategy and the strategies of others. And, this fitness formulation must describe how these payoffs translate into changes in strategy frequencies. The fitness generating function, or *G*-function, provides this service for evolutionary game theory.

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1. Introduction

The *G*-function and its role in modeling strategy dynamics and evolutionary game theory forms the topic of this paper. We will show under what circumstances an evolutionary game can be formulated by a *G*-function [1–3], and how the *G*-function relates to Darwinian dynamics and the concept of evolutionarily stable strategies (ESS [4,5]). There are two components to Darwinian dynamics: population dynamics and strategy dynamics. Because the term adaptive dynamics is often used to describe both

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strategy dynamics and Darwinian dynamics [6–14] we avoid using this term. We view the ESS concept as containing Maynard Smith's original idea of a strategy, which when common, cannot be invaded by rare alternative strategies. We also require that an ESS be a likely outcome of natural selection via Darwinian dynamics when strategy values start near their ESS values. With the G -function we seek to understand:

1. Fit of form and function: How natural selection influences the heritable characteristics of organisms and makes them more suited to their physical and biotic environments. To do this we will discuss the ESS maximum principle and how at the ESS, each strategy of the ESS must maximize the G -function with respect to the individual's strategy.
2. Coevolution: How natural selection determines the reciprocal evolutionary responses of two or more species to each other. We will discuss and illustrate how the ESS that emerges from a single G -function may contain two or more strategies. Insofar as these coexisting strategies represent species, their strategy values with respect to each other represents coevolution [6,15,16]. Furthermore, different species may be represented by different G -functions [17–19]. In which case, species diversity at the ESS can emerge from both within and among G -functions (e.g. [17,20]).
3. Speciation: How Darwinian dynamics can produce forms of adaptive speciation such as sympatric speciation [21–23] or competitive speciation [24–26]. When the number of species allowed within the G -function is less than the number at the ESS, then evolution by natural selection favors speciation by actually driving a species' strategy to a point of minimum fitness and disruptive selection [3,27,28].
4. Macroevolution: Within evolutionary game theory, macroevolution may be usefully defined as evolutionary changes of the G -function itself or changes in its associated strategy set. These changes presumably occur at a much slower and less predictable fashion than microevolutionary changes in strategy that occur within a G -function and its associated strategy set (see [29]).

In what follows, we will show how evolution by natural selection is a game, and how the G -function captures this evolution in a general framework. Next, we show how one takes an ecological scenario and model, conjoin this with evolving traits and produce a G -function for the resulting evolutionary game. Such a game may require just a single G -function if all individuals, irrespective of their current strategies, share the same set of feasible strategies and experience the same fitness consequences from possessing these strategies. When individuals share quite different strategy sets and ecologies, then the evolutionary game may require two or more G -functions. Specifically, we advocate keeping the ESS definition current with advances since Maynard Smith and Price's [4] original. To be a likely outcome of evolution by natural selection, we require that an ESS be resistant to invasion (ESS Maximum principle) and convergent stable with respect to Darwinian dynamics (continuous evolutionary stability of Eshel [30,31]). We then consider a Lotka–Volterra model of competition and a predator–prey model to illustrate the ESS solutions of evolutionary games with one or two G -functions, respectively.

2. Modeling natural selection with the G -function

How does one incorporate the evolutionary process into a dynamical system model? We start with the hypotheses that evolution by natural selection is a special type of game in which the players are individual

organisms and their strategies are heritable phenotypes (see [8,32,33] for comparisons to genetic models of evolution). In the evolutionary game, players inherit their strategies rather than choosing them; and since the evolutionary game has no specific ending, we cannot speak of winners, but rather, of survivors. Not the survival of individuals, but the survival of strategies. Otherwise, the usual characteristics that define a game still exist [34]: individuals play the game by virtue of possessing strategies, and they receive payoffs in terms of fitness functions, where fitness is defined as the per capita growth rate of a strategy. The expected fitness of an individual depends not only on its strategy but on the strategies of other players (frequency-dependence). Generally, an individual's fitness also depends on other ecological factors such as population density (density-dependence).

Because the evolutionary game is not a standard mathematical game such as those found in economics, military sciences, and engineering one cannot directly apply classical game-theoretic methods. For example, suppose a population contained individuals with n different strategies. In order to determine the phenotypes which would survive in this population, it might be tempting to define n different fitness functions and seek a Nash [35] solution (a classic game theoretic solution in which individuals using a given strategy cannot increase their payoff by unilaterally changing their strategies) among the n fitness functions. This approach has two major problems. First, the strategies may exist along a continuum (e.g. body size) in which case the number of potential strategies is infinite and the number of fitness functions necessary to describe a population may be inordinately large. To circumvent this problem, we use the fitness generating function which implicitly includes all potential strategies. Second, a Nash solution from among these fitness functions does not necessarily identify the surviving strategies. For this problem, we need the ESS concept and the ESS Maximum Principle.

2.1. Collapsing a population's fitness functions into a single G -function

Consider a population composed of individuals with n different scalar strategies. Let all of the strategies in the population be given by the column vector:

$$\mathbf{u} = [u_1 \ \cdots \ u_n]^T,$$

where the strategies u_i ($i = 1, \dots, n$) represent a heritable characteristic such as body size. More generally, the full characterization of an organism requires a vector-valued strategy whose dimension equals the number of independent, heritable traits comprising the organism such as the shape of a fish in terms of length, depth, and breadth [36]. We will introduce this generalization later.

Let the population size of each strategy present in the population be given by

$$\mathbf{x} = [x_1 \ \cdots \ x_n]^T,$$

where x_i gives the current number of individuals with strategy u_i . If we let $H_i(\mathbf{u}, \mathbf{x})$ be the individual fitness function of those using strategy u_i , then by definition of fitness (per capita growth rate) changes in strategy population sizes are given by the following:

$$\dot{x}_i = x_i H_i(\mathbf{u}, \mathbf{x}) \tag{1}$$

for continuous-time systems. In Eq. (1), fitness is defined as the per capita growth rate of those individuals using strategy u_i . The methods discussed in the following sections can also apply to discrete-time systems where fitness is defined as the finite growth rate [37].

We can let the above system determine the equilibrium point at which only one or several strategies coexist in the population. But, does this equation predict the outcome of evolution by natural selection and is this an efficient way to model evolution within a population? The answer to both is “No”. The above system of equations only considers the outcome for those strategies already resident in the population and does not consider, nor can it consider, the potentially infinite number of feasible strategies that may occur in the future via selection and/or mutation. Furthermore, we have not taken advantage of the fact that each individual is not a distinct evolutionary lineage but rather shares an evolutionary history and context with others in the population via common ancestry and interbreeding. While distinctive in current strategy, the individuals within a population may be evolutionarily identical. We call a group of individuals evolutionarily identical if their strategies are drawn from the same set of evolutionarily feasible strategies and if the individuals experience the same fitness consequences of possessing the same strategy [1,2]. This creates a special type of symmetric game in which individuals that are evolutionarily identical are completely interchangeable and it is only their strategy which is relevant to determining fitness. For instance, breeds of domestic dogs are probably evolutionarily identical despite the broad range of strategies found among existing breeds. For populations of individuals that are evolutionarily identical, we require just a single fitness generating function to describe the fitness of all of the evolutionarily feasible strategies (resident or otherwise) within the population. In relation to the individual fitness functions, the *fitness generating function* [1,2] is defined as

$$G(v, \mathbf{u}, \mathbf{x})_{v=u_i} = H_i(\mathbf{u}, \mathbf{x}), \quad i = 1, \dots, n,$$

where $u_i \in \mathcal{U}$, the set of all evolutionarily feasible strategies available to the population via reversible and repeatable mutations.

The fitness generating function encapsulates Darwin’s three postulates (adapted from Lewontin [38]) of (1) heritable variation, (2) struggle for existence, and (3) heritable variation influences the struggle into one constructive concept. Heritable variation says that individuals possess strategies; these strategies come from a set \mathcal{U} of evolutionarily feasible strategies. The struggle for existence recognizes that the densities and characteristics of others in the population influences the expected per capita growth rate of an individual: (\mathbf{u}, \mathbf{x}) influences fitness. Heritable variation influences the struggle recognizes that the individual’s strategy matters and influences fitness: $G(v, \mathbf{u}, \mathbf{x})$. The first argument of G is the strategy of the individual under consideration, also called the focal individual. The variables \mathbf{u} and \mathbf{x} represent the current biotic environment that influences fitness.

The earliest forms of G -functions can be found in the evolutionary analyses of the 1970s [20,39,40]. Roughgarden [41] proposed an evolutionary model that does not include the strategy of the focal individual, v . This formulation applies only in the absence of frequency-dependence among individuals with the same strategy. But under frequency-dependence [6,33,42], such a formulation becomes a model of group selection and illustrates the need to have a G -function that separates the strategy of the individual, v , from the strategies used by that individual and others, \mathbf{u} . The formalization of G -functions occurred in the 1980s [1,2,15,24]. And, their application in the 1990s is extensive in works on adaptation, coevolution and adaptive dynamics [3,17,10,11,14,18,19,28].

3. Recipes for evolutionary games using G -functions

The recipe for describing an evolutionary game based on G -functions comes in three steps:

1. Select an ecological model of population dynamics. The model may be for a single population or species, it may be a life-history model with different age and stage classes, or it may be a model of population interactions and include a series of growth equations for several competitors, for their resources, and/or for their predators.
2. Select the scalar or vector-valued strategies and strategy sets associated with the population, species, or community under consideration. The strategy(ies) must have relevance for fitness and population dynamics. The strategy set represents hypotheses concerning genetic, developmental, physiological, and physical constraints on the set of evolutionarily feasible strategies. The strategy set may contain several discrete strategies (matrix games), prescribe feasible combinations of strategies based on equality constraints (e.g. heterozygosity, dominance, penetrance, etc. from Mendelian genetics), or contain continuous strategies upper- and lower-bounded by inequality constraints (akin to some quantitative genetic constraints). At the stage of defining strategies and strategy sets, one decides whether the model calls for one, two or several distinct sets of evolutionarily identical individuals. For instance in a single model of density-dependent population growth, all individuals might be considered evolutionarily identical in which case there is a single strategy set that will become associated with a single G -function. However, in a model of trophic interactions, it may be conjectured that the prey represent one set of evolutionarily identical individuals (a small mammal for instance) and the predators another (a raptorial bird). In this case, there will be a separate strategy set and G -function associated with each group of evolutionarily identical individuals.
3. Create the G -function(s) by hypothesizing how the individual's strategy, v , and the strategies of others, \mathbf{u} , influence the values of parameters in the ecological models of population dynamics. As soon as key parameters of a population model become functions of v , \mathbf{u} , \mathbf{x} , the ecological model may be described in terms of a G -function.

The Lotka–Volterra model is an example of competition formulated as a single G -function with a scalar strategy [6]:

$$G(v, \mathbf{u}, \mathbf{x}) = r \left[\frac{K(v) - \sum x_i a(v, u_i)}{K(v)} \right], \quad (2)$$

where the G -function embodies the assumption that carrying capacity, $K(v)$, is a function of the individual's strategy, and that competitive interactions, $x_i a(v, u_i)$ are a function of the individual's strategy and the strategies and population sizes of the competitors.

4. Types of G -functions

The form and complexity of the G -function will depend on the complexity of the community under consideration. We have already illustrated how the G -function can be used to model a community of evolutionarily identical species using a scalar evolutionary parameter. Using appropriate notation, the G -function concept can be extended to include vector evolutionary parameters, groups of different

evolutionarily identical individuals and communities with multiple stage life histories. However, the notation becomes burdensome if we try to incorporate all options at once. We will therefore look at these options one after the other.

4.1. A single G -function

If all individuals are evolutionarily identical and share the same G -function, we can model the evolution of a vector-valued strategy by extending the notation of \mathbf{u} . In this case, let $\mathbf{u}_1, \dots, \mathbf{u}_n$ be the strategy vectors with components

$$\mathbf{u}_i = [u_{i1} \cdots u_{ic}],$$

where c is the number of components associated with the strategy vectors \mathbf{u}_i . Since all the individuals are evolutionarily identical, c has the same value for all i . We may now define

$$\mathbf{u} = [\mathbf{u}_1 \cdots \mathbf{u}_n]^T$$

as the column vector of all the components of all the strategy vectors. Under this notation, the complete specification of strategies within a population is visualized as a vector of vectors (each sequence of vectors representing the different traits of a strategy, for instance the first set of c components belong to x_1 , the second c components belong to x_2 and so on).

As an example consider the Lotka–Volterra competition model formulated as an evolutionary game with vector-valued strategies. Imagine that carrying capacity, K , is a bi-normal function of the two components of a vector-valued strategy. This model considers a two dimensional niche space where each strategy influences carrying capacity and competition along one of the niche axes. The model can be given by

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

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

$$\alpha(\mathbf{v}, \mathbf{u}_j) = 1 + \exp\left[-\frac{((v_1 - u_{j1}) + b(v_2 - u_{j2}) + \beta)^2}{2\sigma_\alpha^2}\right] - \exp\left[-\frac{\beta^2}{2\sigma_\alpha^2}\right].$$

In the above, v is a vector with the two components v_1 and v_2 . The terms a and b scale the effect of the second strategy component on carrying capacity and competition, respectively. For illustration we have shown both carrying capacity and competition coefficients as bi-normal functions of the two strategy components. Both strategy components will be subject to evolution, 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. The above model can be easily modified (by means of summations)

to consider any c -dimensional niche space with any number of components forming the traits of the vector-valued strategy, $v = v_1, \dots, v_c$.

4.2. Multiple G -functions

We can model the evolutionary ecology of individuals drawn from two or more sets of evolutionarily identical individuals by specifying two or more G -functions and strategy sets for each group of individuals. Since we are increasing the notational burden with the addition of multiple G -functions, we will decrease this burden by assuming that the strategies are again scalars. In this case u_{ij} is the i th strategy of the j th G -function,

$$\mathbf{u}_j = [u_{1j} \ \cdots \ u_{n_j j}]^T,$$

where n_j designates the number of extant strategies within the j th G -function. The vector of all strategies is given by

$$\mathbf{u} = [\mathbf{u}_1 \ \cdots \ \mathbf{u}_{n_b}]^T,$$

where n_b designates the number of G -functions.

Let x_{ij} be the i th population size from the j th G -function,

$$\mathbf{x}_j = [x_{1j} \ \cdots \ x_{n_j j}]^T$$

and

$$\mathbf{x} = [\mathbf{x}_1 \ \cdots \ \mathbf{x}_{n_b}]^T$$

be the vector of all populations.

If we designate the fitness function for the i th population in the j th G -function as H_{ij} then under this notation the j th G -function is defined by

$$G_j(v_j, \mathbf{u}, \mathbf{x})_{v_j=u_{ij}} = H_{ij}(\mathbf{u}, \mathbf{x}), \quad i = 1, \dots, n_j, \quad j = 1, \dots, n_b,$$

where $u_{ij} \in \mathcal{U}_j$ where \mathcal{U}_j is the strategy set corresponding to the j th G -function. Note that the strategy of the focal individual in $G_j(v_j, \mathbf{u}, \mathbf{x})$ is assumed to be a scalar.

Models of predator–prey coevolution provide examples of evolutionary games with two G -functions ([17] also see [7,19]):

$$\text{Prey : } G_1(v_1, \mathbf{u}, \mathbf{x}) = r_1 \left[\frac{K(v_1) - \sum_{i=1}^{n_1} x_{i1} a(v_1, u_{i1})}{K(v_1)} \right] - \sum_{k=1}^{n_2} x_{k2} b(v_1, u_{k2}), \tag{3}$$

where $v_1 \in \mathcal{U}_1$.

$$\text{Predator : } G_2(v_2, \mathbf{u}, \mathbf{x}) = r_2 \left[1 - \frac{\sum_{i=1}^{n_1} x_{i2}}{c \sum_{k=1}^{n_2} x_{i1} b(v_2, u_{i1})} \right] \tag{4}$$

and $v_2 \in \mathcal{U}_2$.

5. The ESS concept and the ESS maximum principle

5.1. Types of evolutionary dynamics

Here we will link the ecological properties of the G -function as a model of population dynamics with its evolutionary properties of predicting changes in strategy frequencies or strategy values. The G -function determines changes in the frequency and population sizes of the extant strategies. However, it does not specify how strategies evolve or how novel strategies become introduced into the population. There are two ways for allowing the population to explore its strategy set: invasion structured evolution and strategy dynamics.

Invasion structured evolution [6,43] means that novel strategies at low frequency are occasionally introduced into the population. The novel strategies may be introduced one at a time, in which case a new strategy is not introduced until the previous novel strategy has either gone extinct or achieved an equilibrium frequency. Or, the novel strategies may be introduced at fixed or random intervals without regard to the current status of previous “mutations”. The former scenario allows for only one mutant strategy at a time whereas the latter scenario permits multiple mutant strategies and allows the number of extant strategies to vary in number. There are two ways of selecting the mutant strategies from the strategy set. Strategies can be selected at random from the entire strategy set without regard to the extant strategies. This allows the population to explore its entire strategy set and this allows for “hopeful monsters” in that novel strategies that are extremely different from the current strategies are just as likely to occur as strategies more similar to the extant strategies. Or, mutant strategies may be restricted to some subset of the strategy set that is in the neighborhoods of the current strategies [44]. This restricts the ability of the population to explore its entire strategy set but it may more realistically reflect the distribution of mutations. Restricting the neighborhood of mutant strategies, in fact, provides one avenue to the following characterization of strategy dynamics [44].

Strategy dynamics fixes the number of extant strategies and then permits these strategies to evolve in directions of higher fitness. The direction and rate of change of u_{ij} is determined by the shape of the adaptive landscape. The adaptive landscape can be visualized by graphing G_j as a function of the individual’s strategy, v_j . Each existing strategy evolves in the direction of the landscape’s gradient and at a rate proportional to the magnitude of the landscape’s slope (see [44,45] for original derivations under small mutations in the neighborhood of an existing strategy). This gives the following strategy dynamic [6,8,44,46]:

$$\frac{du_{ij}}{dt} = s_j \left. \frac{dG_j}{dv_j} \right|_{v_j=u_{ij}},$$

where s_j is a rate constant for the speed of evolutionary change within the j th G -function.

5.2. The ESS concept

Maynard Smith and Price’s [4] pioneering ESS definition states that the ESS is a strategy which when common cannot be invaded by rare alternative strategies. What this means is that at the ESS no strategies have higher fitness and no strategies can increase in frequency. The ESS is resistant to invasion. However, Eshel [30,31] showed how strategies that are resistant to invasion may not necessarily be able to invade or

increase in frequency in populations with strategies very close to the uninvadable strategy. Eshel referred to strategies that are resistant to invasion as “Evolutionarily Unbeatable Strategies”. When such strategies are scalars they must satisfy the following necessary conditions [11]:

$$\left. \frac{dG_j}{dv_j} \right|_{v_j=u_{ij}} = 0, \quad \left. \frac{d^2G_j}{dv_j^2} \right|_{v_j=u_{ij}} < 0.$$

When Darwinian dynamics result in evolution by natural selection converging on a particular strategy, Eshel referred to such a strategy as a “continuously stable strategy”. Such a strategy may not necessarily be an “evolutionarily unbeatable strategy” in that it can be invaded by one or combinations of mutant strategies. Metz et al. [11] and Cohen et al. [3] give the necessary conditions for convergence stability when there is a single G -function with a scalar-valued strategy.

While it is true that Maynard Smith’s [5] definition for the ESS only insures resistance to invasion, convergence stability must clearly be part of the spirit of the ESS concept. To be a likely consequence of evolution by natural selection, an ESS must be resistant to invasion and must also result from Darwinian dynamics in the neighborhood of the ESS. We find the following definitions that leads to such an ESS to be the most useful.

First, an ESS must be ecologically stable in the sense that the strategy or strategies of the ESS must be able to persist together through time. To capture the ecological stability of the ESS we use the concept of an Ecologically Stable Equilibrium. A term first coined and defined by Goh [47] and then reformulated by Vincent et al. [48] specifically for the evolutionary game.

Given a strategy vector $u \in \mathcal{U}$, suppose that there exists a corresponding ecological equilibrium point x^* in the population space with the property that $H_i(u, x^*) = 0$ for $i = 1, \dots, \sigma \geq 1$ and $x_i^* = 0$ for the indices $\sigma + 1, \dots, n$. In other words, at least one population must have a non-zero equilibrium, but all the others may be zero. In this case, x^* is said to be an ecologically stable equilibrium (ESE) if the population dynamics returns to this point from any allowable initial condition in the population space (i.e. $x(0) > 0$, local or global as specified). The important point in this definition is that u is held fixed and the system returns to x^* with the same conditions on H_i and those components of x_i^* which are zero regardless of the value chosen for $n \geq \sigma$.

Next, we need to consider both the strategies that will comprise the ESS and all possible mutant strategies that might occur via invasion structured evolution or strategy dynamics. Toward this end we define a coalition vector of strategies as being those strategies associated with the non-zero populations at the ecological equilibrium point. In other words a coalition vector is $u_c = [u_1, \dots, u_\sigma]$. We designate the remaining strategies by $u_m = [u_{\sigma+1}, \dots, u_n]$.

Finally, for a coalition vector to be an ESS it must be resistant to invasion from any set of alternative strategies, and able to return to the ESS if perturbed slightly with respect to population sizes of either the coalition strategies or alternative strategies. A coalition vector $u^* \in \mathcal{U}$ is said to be an evolutionarily stable strategy (ESS) for the equilibrium point x^* if, for all $n > \sigma$ and all strategies $u_m \in \mathcal{U}$, the equilibrium point x^* remains an ecologically stable equilibrium (ESE).

The ESS will be a local ESS if x^* is a local ESE and the ESS will be a global ESS if x^* is a global ESE. Note that under this definition an ESS must be an ESE, but an ESE is not necessarily an ESS. According to this definition the ESS need only be local with respect to population sizes, x^* , but global with respect to strategy, u^* .

If we go back to the original word definition of an ESS given by Maynard Smith [5], “an ESS is a strategy such that, if all members of a population adopt it, then no mutant strategy could invade the population under the influence of natural selection”, we see that the above ESS definition includes Maynard Smith’s definition but it has been expanded. The ESS may now be a coalition of strategies and the ESS must be convergent stable as well as resistant to invasion.

5.3. ESS maximum principle

For a strategy or set of strategies to be an ESS, the strategies must reside at global maxima of the adaptive landscape when the population is at the ESS. So, while frequency-dependent selection may not optimize any population measures of fitness, it does optimize an individual measure of fitness in the context of the G -function. In this way the G -function allows one to solve evolution’s hermeneutic circle. The inner evolutionary game relates how the current state of the population influences the fitness of the individual’s strategy, and in the outer game these fitnesses influence the composition of the population with respect to strategies and population sizes (sensu Vincent and Brown [2]). As the inner and outer game cycle through this evolutionary hermeneutic circle the resultant strategies will likely be ESS and maximize G with respect to v at (u^*, x^*) . We have arrived at this result in several papers. Most recently [48] we have stated it as the ESS Maximum Principle. The principle states that if $G(v, \mathbf{u}, \mathbf{x})$ [or $G_j(v_j, \mathbf{u}, \mathbf{x})$] is a fitness generating function for a community and if u^* is an ESS, then $G(v, \mathbf{u}^*, \mathbf{x}^*)$ must take on a maximum value of zero with respect to $v \in \mathcal{U}$ at u_1, \dots, u_σ [or $G_j(v_j, \mathbf{u}, \mathbf{x})$ must take on a maximum value of zero with respect to $v_j \in \mathcal{U}_j$ at $u_{1j}, \dots, u_{\sigma j}$ for $j = 1, \dots, n_b$]. In applying this principle one must keep in mind that G is maximized with respect to v while holding $\mathbf{u}^*, \mathbf{x}^*$ fixed and that G will take on a maximum value of zero at each strategy in the coalition vector \mathbf{u}^* . This may seem strange at first since, after all, the value of v which maximizes G is contained in \mathbf{u}^* . One must be careful in applying the principle to perform the optimization in terms of the explicit v contained in G .

6. Example 1: a Lotka–Volterra model of evolution and coevolution of competitors

The G -function constructed around the Lotka–Volterra model of competition provides an example of an evolutionary game with a single G -function.

6.1. Model description

We will consider the different extant strategies and population sizes as different species. Let the individual’s strategy, v , influence its carrying capacity, $K(v)$, according to the following [41,49]:

$$K(v) = K_m \exp \left[-\frac{v^2}{2\sigma_k^2} \right],$$

where K_m is the maximum achievable carrying capacity and σ_k^2 determines how quickly the carrying capacity of an individual declines as its strategy deviates from the strategy that maximizes carrying capacity, $v = 0$.

Let the intensity of competition be determined by the combination of the individual’s strategy and the strategy of others [6,9]:

$$a(v, u_i) = 1 + \exp \left[-\frac{(v - u_i + \beta)^2}{2\sigma_a^2} \right] - \exp \left[-\frac{\beta^2}{2\sigma_a^2} \right],$$

where σ_a^2 determines how quickly the intensity of competition declines as the individual’s strategy deviates from the strategy of others that maximizes competition, $u_i = v + \beta$. The term β makes competition asymmetric. When $\beta=0$ then competition is symmetric, when $\beta > 0$ then individual’s with larger strategies have a greater competitive effect on individuals with smaller strategies and vice-versa. The last term on the RHS scales competition so that it takes on a value of 1 when $v = u_i$, and it opens up the possibility that individuals may actually have a positive effect on others. Biologically, this might occur when sufficiently divergent competitors actually benefit each others growth rates via indirect mutualism.

6.2. Finding the ESS

We first look for an ESS coalition of 1 ($\sigma = 1$) by modifying the G -function to include just one extant strategy, u_1 , at its equilibrium population size, $x_1^* = K(u_1)$:

$$G(v, u_1, x_1^*) = r \left[\frac{K(v) - \alpha(v, u_1)K(u_1)}{K(v)} \right].$$

Maximizing G with respect to v and evaluating at u_1 requires

$$\left. \frac{\partial G}{\partial v} \right|_{v=u_1=u_1^*} = 0$$

which yields the ESS candidate solution

$$u_1^* = \beta \left(\frac{\sigma_k}{\sigma_\alpha} \right)^2 \exp \left[-\frac{\beta^2}{2\sigma_\alpha^2} \right]. \tag{5}$$

When an ESS coalition of 1 solution exists ($\sigma = 1$), if it is global (Fig. 1a), then it follows from the definition of an ESS that ESS coalitions greater than one ($\sigma > 1$) cannot exist. When an ESS is global with respect to initial strategy frequencies, it is not possible to have ESS coalitions of $\sigma_1 = 1$ and $\sigma_2 = 2$ simultaneously. This is because the ESS is convergent stable regardless of the initial conditions on strategy numbers (so long as there are at least as many strategies as the ESS coalition) and strategy frequencies.

6.3. The solution for the group optimum

Let us compare the above ESS solution with a solution that maximizes the individual fitness function with respect to the population’s strategy \mathbf{u} . Such a solution requires that an ecological equilibrium for each surviving strategy maximizes H_i with respect to u_i . If only one species is present, ($\sigma = 1$) the fitness function for this species is given by

$$H_1 = r \left(\frac{K(u_1) - rx_1}{K(u_1)} \right).$$

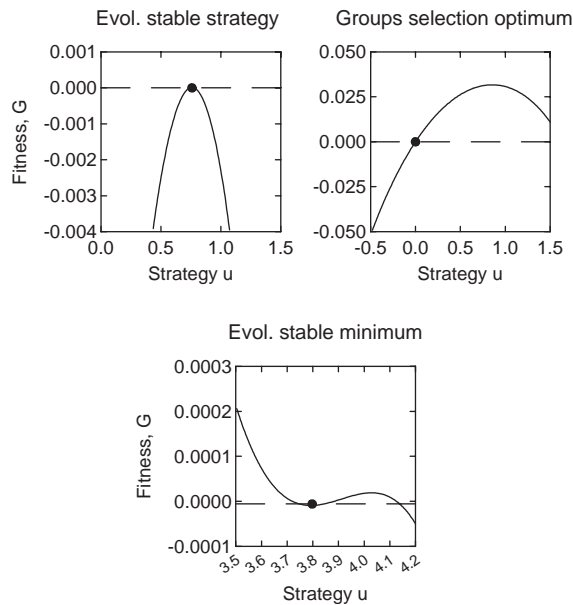


Fig. 1. Two outcomes of Darwinian dynamics when the entire population shares the same strategy. The single strategy evolves to a global ESS ($u_1 = 1.213, x_1 = 83.2$) when the niche axis is quite peaked ($\sigma_k^2 = 4$). Under a broader niche axis ($\sigma_k^2 = 12.5$) the single strategy evolves to an evolutionarily stable minimum ($u_1 = 3.791, x_1 = 56.28$). While this strategy is convergent stable it is highly invadable by an additional strategy or prone to adaptive speciation due to disruptive selection. For this example and those in Figs. 2 and 3, $K_{max} = 100$ and $R = 0.25$.

Maximizing H_1 with respect to u_1 requires

$$\left. \frac{\partial H_1}{\partial u_1} \right|_{x^*=K(u_1)} = 0$$

which yields

$$u_1 = 0; x_1 = K_m.$$

While this strategy maximizes equilibrium population size, it is not an ESS and as can be seen from the adaptive landscape at this point (Fig. 1b) this strategy can be invaded by strategies with values greater than 0. As is often the case under frequency-dependent selection, evolution by natural selection does not produce a strategy that maximizes any group measure of fitness, despite the fact that the G -function does take on a maximum with respect to v .

6.4. A coalition of two or more strategies at the ESS

By making σ_k^2 sufficiently large, the candidate ESS described by (5) no longer maximizes G^* but rather minimizes G^* with respect to v evaluated at $v = u_1$ (Fig. 1c). Interestingly, the candidate ESS solution is still convergent stable. If we restrict the population to a single extant strategy, then Darwinian dynamics will result in u_1 even though it represents a fitness minima on the adaptive landscape. Hence, if the number

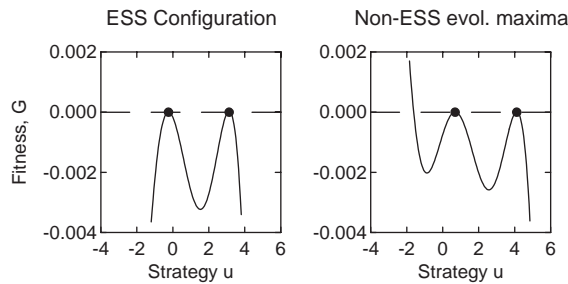


Fig. 2. Two outcomes of Darwinian dynamics when the community is composed of two evolving strategies (= species in this example). The two strategies evolve to a global ESS ($u_1 = -0.240, u_2 = 3.129, x_1 = 39.28, x_2 = 51.06$) when the niche axis is moderately broad ($\sigma_k^2 = 12.5$). Under a still broader niche axis ($\sigma_k^2 = 18$) the two strategies evolve to two local maxima ($u_1 = 0.691, u_2 = 4.116, x_1 = 50.25, x_2 = 41.42$). While these strategies are convergent stable they can be invaded by strategies sufficiently smaller than u_1 .

of extant strategies is restricted it is possible to have an evolutionarily stable minimum (sensu Abrams et al. [28], see also [9,27]). But, the strategy is not resistant to invasion and it is not an ESS. The number of extant strategies can either be increased by permitting competitive speciation [11,16,24,26,50] or by permitting the invasion of a novel strategy. Both may be likely implications of an evolutionarily stable minimum. Speciation may be likely because adaptive dynamics hold the single strategy at a point of disruptive selection, and invasion is likely because any novel strategy in the neighborhood of the existing strategy will have higher fitness.

If we consider a coalition of two strategies, $\mathbf{u} = (u_1, u_2)$, then we can write G as:

$$G(v, \mathbf{u}, \mathbf{x}^*) = r \left[\frac{K(v) - \alpha(v, u_1)x_1^* - \alpha(v, u_2)x_2^*}{K(v)} \right]$$

and the first order necessary conditions require that for $i = 1, 2$:

$$\left. \frac{\partial G}{\partial v} \right|_{v=u_i} = 0.$$

As individuals experience a smaller decline in carrying capacity as their strategy deviates from $v = 0$ (larger values for σ_k^2), the competition model of Fig. 1 switches from an ESS coalition of one species to an ESS coalition of two species ($\partial^2 G / \partial v^2|_{v=u_1}$ switches from negative to positive). The two species ESS generates an adaptive landscape with two equal peaks at the ESS when the population is using the ESS, $(\mathbf{u}^*, \mathbf{x}^*)$ (Fig. 2a). At still larger values for σ_k^2 , the ESS candidate coalition of two species continues to be convergent stable but ceases to be an ESS (Fig. 2b). At this point the ESS coalition contains 3 species (Fig. 3a), and as σ_k^2 becomes even larger the candidate ESS of three species remains convergent stable (Fig. 3b) but the ESS coalition keeps growing in the number of species. In fact when the ESS contains four species, there exists a convergent stable coalition of one species, two species, three species, as well as the actual ESS of four species. The ESS and candidate ESS for coalitions of more than one species were found using a combination of invasions, and strategy dynamics. As an interesting aside, invasion structured evolution seems to be the most effective way of increasing the number of extant strategies and for exploring the entire strategy set. On the other hand, strategy dynamics are very effective at obtaining the ESS once the number of strategies and their values are in the neighborhood of an ESS. Also, using

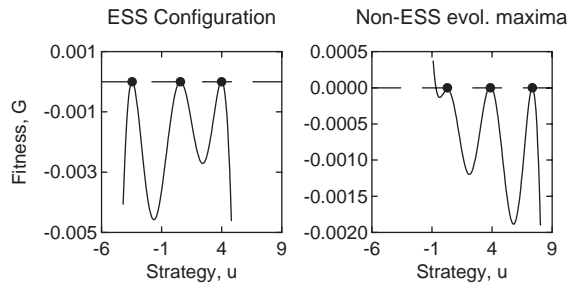


Fig. 3. Two outcomes of Darwinian dynamics when the community is composed of three evolving strategies (= species in this example). The three strategies evolve to a global ESS ($u_1 = -3.459, u_2 = 0.5605, u_3 = 3.988, x_1 = 6.87, x_2 = 47.75, x_3 = 41.59$) when the niche axis is broad ($\sigma_k^2 = 18$). Under a still broader niche axis ($\sigma_k^2 = 50$) the three strategies evolve to three local maxima, respectively, ($u_1 = 0.284, u_2 = 3.860, u_3 = 7.358, x_1 = 44.20, x_2 = 40.21, x_3 = 24.06$). While these strategies are convergent stable they can be invaded by strategies sufficiently smaller than u_1 .

strategy dynamics seems to be an effective means for determining whether coalitions with fewer strategies than the ESS coalition are convergent stable (e.g. evolutionarily stable minima).

Models like the Lotka–Volterra competition model discussed in this section provide models of an adaptive radiation. When the ESS coalition possesses say four species, we can start with a single species that evolves to an evolutionarily stable minimum. At this point competitive speciation or an invasion increases the coalition to two species that can evolve to a new convergent stable point. This succession of speciation combined with evolution towards convergent stable points can eventually lead to the ESS of four species (for other examples of speciation and evolutionary branching see [25,26,51]).

7. Example 2: predator–prey coevolution

We can apply the same combination of analytical tools, invasion structured evolution, and adaptive dynamics to consider the ESS for the predator–prey model of coevolution given by Eqs. (3) and (4).

7.1. The model

For the prey assume the same functional forms as above for $K(v_1)$ and $\alpha(v_1, u_{i1})$ with exception that competition is symmetric ($\beta = 0$). Let an individual prey’s risk of capture by a predator individual be a function of its strategy, v_1 , and the predator’s strategy, u_{k2} :

$$b(v_1, u_{k2}) = b_m \exp \left[-\frac{(v_1 - u_{k2})^2}{2\sigma_p^2} \right],$$

where b_m is the maximum per capita rate of prey capture by an individual predator, and σ_p^2 determines how quickly the predator’s capture rate declines as its strategy deviates from that of the prey. This model assumes that the predator maximizes its capture rate by matching the prey’s strategy. From the perspective of

an individual predator the above equation reads:

$$b(v_2, u_{i1}) = b_m \exp \left[-\frac{(v_2 - u_{i1})^2}{2\sigma_p^2} \right].$$

7.2. Finding the ESS

We first look for an ESS coalition of 1 prey and 1 predator species ($\sigma_1 = \sigma_2 = 1$) by modifying the G -function to include just one extant prey strategy, u_{11} , one extant predator strategy, u_{12} , and their respective equilibrium population sizes, x_{11}^* and x_{12}^* , respectively. We refer to these modified G -functions as G_1^* and G_2^* , respectively,

$$\text{prey : } G_1(v_1, \mathbf{u}, \mathbf{x}^*) = r_1 \left(\frac{K(v_1) - \alpha(v_1, u_{11})x_{11}^*}{K(v_1)} \right) - b(v_1, u_{12})x_{12}^*,$$

$$\text{predator : } G_2(v_2, \mathbf{u}, \mathbf{x}^*) = r_2 \left[1 - \frac{x_{12}^*}{cx_{11}^* \beta(v_2, u_{11})} \right].$$

For this example, maximizing G_1 with respect to v_1 and G_2 with respect to v_2 requires for $j = 1, 2$:

$$\left. \frac{\partial G_j}{\partial v_j} \right|_{v_j=u_{1j}} = 0.$$

At the solution shown in Fig. 4a, the single prey species takes on a strategy that maximizes its carrying capacity and the predator takes on a strategy that maximizes its capture rate on the prey. The predator has “won” the coevolutionary game in that it has perfectly matched the prey’s strategy. The prey experience disruptive selection from the predators. Any shift (up or down) in prey strategy will reduce the mortality rate from predators. However, having lost to the predator, the prey is compensated with the highest achievable carrying capacity. The candidate solution of $u_{11} = u_{12} = 0$ is a global ESS for this model so long as, from the prey’s perspective, the stabilizing selection from maximizing carrying capacity exceeds the disruptive selection induced by the predators (Fig. 4b). As soon as the prey experiences a sufficiently large disruptive selection from the predator (which occurs as the predator’s niche breadth, σ_p^2 , declines), the effect of the prey’s strategy switches from maximizing to minimizing G_1^* (Fig. 4b).

As the predator’s niche breadth declines, the candidate solution of $u_{11} = u_{12} = 0$ yields an evolutionarily stable maximum for the predators but an evolutionarily stable minimum for the prey. At this point, we can expect competitive speciation or the invasion of an alternative prey strategy to free the single prey species from its evolutionary purgatory. Following speciation, there exists a global ESS with one predator species and two prey species (Fig. 4c). The predator’s niche breadth is an evolutionary bifurcation parameter for the diversity of prey and predator species. In the community of two prey and one predator species, the predator now experiences disruptive selection from the opposing selective pressures exerted by the prey on the predator. At a sufficiently narrow predator niche breadth, this disruptive selection is sufficiently strong to switch the single predator’s strategy from an evolutionarily stable maximum to an evolutionarily stable minimum. Competitive speciation allows system to evolve, via adaptive dynamics, to a new global ESS of two prey and two predator species (Fig. 4d).

Continued reductions in the predator’s niche breadth will continue the successive increases in the numbers of prey and predator species within the community [17]. At all of these ESS solutions where

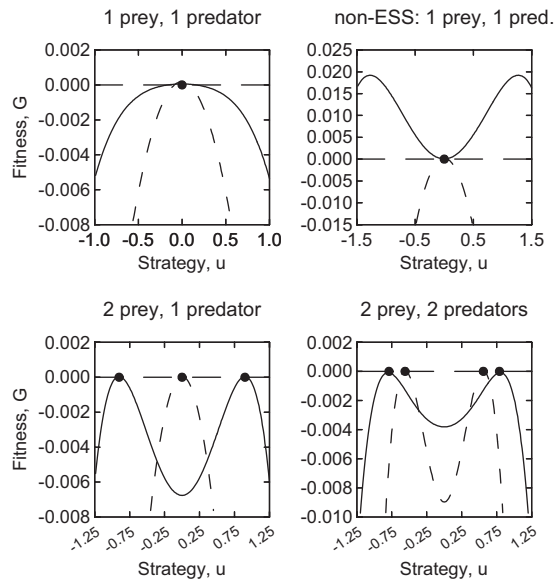


Fig. 4. Some of the outcomes of Darwinian dynamics for the predator–prey model. When the predators have a broad niche breadth ($\sigma_p^2 = 10$), the ESS contains a single prey and a single predator species. Under a narrower niche breadth ($\sigma_p^2 = 4$), the single prey evolves to an evolutionarily stable minima while the single predator species evolves to a maximum of its adaptive landscape. This is not ESS as the prey can be invaded by alternative strategies, or the single prey strategy may undergo adaptive speciation. Under this narrower niche breadth, the ESS contains two prey species and a single predator species. Under still narrower niche breadth ($\sigma_p^2 = 1$), the ESS contains two prey species and two predator species.

the strategies are on the interiors of the prey and predator strategy sets, the following necessary condition applies for all prey and predator strategies within the ESS:

$$\left. \frac{\partial G_1}{\partial v_1} \right|_{v_1=u_{i1}} = 0,$$

$$\left. \frac{\partial G_2}{\partial v_2} \right|_{v_2=u_{k2}} = 0,$$

where $i = 1, \dots, \sigma_1$ and $j = 1, \dots, \sigma_2$ refer to the prey species and predator species within the ESS coalition, respectively. With several G -functions the ESS may contain a diversity of strategies, both within and between G -functions.

8. Conclusion

When density-independent, natural selection promotes the strategy that maximizes population growth rate [52]; ecologically this is r -selection. When density-dependent, natural selection promotes the strategy that maximizes equilibrium population size; ecologically this is K -selection [41,53–55]. When selection is frequency-dependent, the hermeneutic circle of evolution by natural selection becomes more enigmatic and diverse in outcome. Traditional fitness functions based on population growth rate, or quantitative

genetic dynamics become inadequate or unrevealing for this case. Under frequency-dependence, the fitness generating function, or G -function, provides an appropriate measure of fitness for determining the ecological and evolutionary dynamics. The G -function defines fitness as the per capita growth rate of a strategy in the context of the values and densities of extant strategies. Evolution is defined as change in strategy frequency. In this context, neither individuals nor groups have fitness. Rather, strategies have fitness. If a strategy is a property of the individual then evolution can be thought of as “individual selection”, and if strategies are the properties of groups (or genes) then evolution is “group selection” (or genic selection). The variables of the G -function include the strategies currently found within the population, \mathbf{u} , the densities of individuals with each strategy, \mathbf{x} , and the strategy of the focal individual, v . The terms \mathbf{u} and \mathbf{x} describe the current biotic state of the population or community. Setting v equal to one of the extant strategies within \mathbf{u} allows G to return the per capita growth rate of the individuals using that strategy. Moreover the G -function can be used to evaluate the potential fitness of any strategy from the strategy set, \mathcal{U} , whether or not the strategy currently exists within the population. This property of G -functions allows us to plot the frequency-dependent adaptive landscape by graphing G as a function of v for a given biotic environment, (\mathbf{u}, \mathbf{x}) . At an ESS under frequency-dependent selection, evolution by natural selection maximizes the fitness generating function with respect to the individual’s strategy v .

To model evolution using G -functions, one begins with a single model or set of models of population dynamics. Within a G -function, all individuals share the same set of evolutionarily feasible strategies and have their expected fitness determined by the same fitness generating function. For example, all species and members of the dog family, Canidae, are probably part of the same G -function. Whereas members of the cat family, Felidae, probably represent a separate G -function. A fox cannot repeatedly and reversibly be evolved into a house cat or vice-versa. Consider natural selection acting on a fox or a house cat to fill the tiger niche. Arguably, in the case of the cat one would probably arrive at a tiger whereas in the case of the fox one would probably achieve a tiger-like canid, not a morphologically correct “tiger”. After selecting the number of G -functions for the evolutionary game, the next step is to determine the nature of the strategy(ies). Is the heritable trait scalar valued or vector valued? And, what is the complete set of evolutionarily feasible values for this strategy? Is the set discrete (matrix games [56,57]) or continuous (continuous parametric games [2])? Finally, how does the strategy of the individual, v , the strategy of others, \mathbf{u} , and the densities of others’ strategies, \mathbf{x} , influence the fitness of a strategy? Having defined all of the above, we arrive at a set of fitness generating functions for the system: $G_j(v_j, \mathbf{u}, \mathbf{x})$ where $j = 1, \dots, n_b$ denotes the number of G -functions. The hermeneutic circle is now closed. Through the G -function, the fitness of each strategy is influenced by its biotic environment, and the fitness of each strategy determine changes to this biotic environment.

There are three tools available for determining the outcome of evolution by natural selection in the evolutionary game defined by $G_j(v_j, \mathbf{u}, \mathbf{x})$: (1) ESS Maximum principle, (2) invasion structured evolution, and (3) strategy dynamics, or combinations of all three. While not the only possible outcome, an ESS is a likely outcome of evolution by natural selection, particularly when an ESS is defined as both resistant to invasion (global with respect to \mathbf{u}) and convergent stable (local with respect to \mathbf{x}). The ESS maximum principle can be applied to find (using numerical or analytical techniques) ESS candidate solutions. These candidate solutions can then be tested for convergent stability and resistance to invasion using various perturbation analyses. Invasion structured evolution [6] is an effective way for determining the numbers of strategies at the ESS. As the process of introducing rare alternative strategies proceeds, surviving strategies begin to cluster around the strategies of an ESS. However, the exact values of the ESS remains elusive since the exact ESS values must arise coincidentally and the extinction of nearby

strategies can take a great deal of time. Strategy dynamics is an attractive means for mimicking evolution by natural selection, for evaluating whether candidate ESSs are convergent stable, and for revealing the wider range of outcomes from natural selection under frequency-dependence.

Darwinian dynamics can result in an ESS [9], evolutionarily stable minima [11,27,28], a variety of non-equilibrium strategy dynamics [7,18,46], and locally stable evolutionary maxima [3]. When the number of evolving strategies is less than that of an ESS, then evolution towards evolutionarily stable minima becomes likely. At this point, competitive speciation can result in the split of a strategy into two and evolution may proceed towards an ESS [25,27,58]. However, if the number of starting strategies is less than the number at an ESS and the resultant strategy dynamics are non-equilibrium, then competitive speciation cannot occur and the system cannot evolve to an ESS without the invasion of novel strategies. Furthermore, even if the initial numbers of strategies are sufficient to achieve the ESS, their initial values may preclude Darwinian dynamics from reaching an ESS in which case non-equilibrium strategy dynamics or the extinction of one or more strategies may result from convergent evolution.

In the absence of competitive speciation and invasion-structured evolution, natural selection may result in outcomes that are not ESS. What must nature be like, then, if most ecological systems most of the time are at or near an ESS? We conjecture that an ESS will be the most likely outcome of evolution by natural selection in the presence of Darwinian dynamics, competitive speciation (a strategy will split into two when present at an evolutionarily stable minima), and allopatric speciation (= invasion structured evolution). Whether this conjecture is correct is primarily an empirical question. Evolutionary game theory has shown us how evolution may result in a bestiary of outcomes. It remains to be seen which actually occur regularly in nature. One of evolutionary game's greatest need are clever empirical studies that test among these outcomes.

The modeling of evolution with G -functions is in its infancy. Most of us modelers are like children in a candy shop. By merely creating and doing ever more extravagant things with G -functions, the ESS concept, strategy dynamics, or invasion structuring, we are presented with bizarre and novel possibilities for frequency-dependent selection. We have found that frequency-dependent selection is to density-dependent and density-independent selection as Alice's Wonderland was to her real world. Most evolutionary ecologists come trained with a density-dependent/density-independent mindset of evolution when a frequency-dependent mind set is called for. Under the former mind set, adaptive landscapes are relatively rigid, evolution focuses mostly on the small changes in existing strategies, and the full set of what is evolutionarily feasible is generally ignored. With a frequency-dependent and game-theoretic mind set, adaptive landscapes may be highly variable and dynamic. This fitness surface may change more than the strategies themselves, and an appreciation for the full range of evolutionarily feasible strategies becomes necessary.

In the area of modeling and the biomathematics of evolutionary games much is controversial, conjecture, and incomplete. What happens to the ESS concept and strategy dynamics under non-equilibrium population dynamics? Early work suggests that the evolutionary processes may remain intact by expanding the G -function to include geometric mean fitness over the distribution of expected population sizes [59,60]. But, might non-equilibrium population dynamics and their temporal scale relative to strategy dynamics introduce time-lags or instabilities that decrease the likelihood of achieving or maintaining a community at its ESS? While much of the theory can be extended to vector-valued strategies, few models explicitly evaluate vector-valued strategies (see Brown [61,62]). Vector-valued strategies may facilitate evolution by natural selection towards an ESS by multiplying the range of fitness gradients over which a strategy can traverse the landscape. Or, vector-valued strategies may actually cause a discontinuity in

the landscape that reduces the ability of populations to explore their strategy set via strategy dynamics ([61], e.g. the evolution of niche conservatism, [63–65]). The numbers of G -functions may complicate the analysis of evolutionary outcomes and increase the range of outcomes. To date, the most extensive model of the evolution of community diversity and organization has included just two G -functions [17]. Equally exciting is the modeling of macroevolution by considering how evolution proceeds as a consequence of macroevolutionary shifts in G -functions and their associated strategy sets.

Evolution by natural selection is a kind of hermeneutic circle. It is this self-referential nature of selection in which a strategy is both defined by its context and defines its evolutionary context that magnifies the richness, complexity and beauty of the natural order. It may also cause despair at ever applying a “simplistic” Darwinian approach to understanding nature. But, regardless of the amount of self-referencing in nature, the Malthusian and Darwinian Laws of evolution do apply, and tools such as G -functions and evolutionary game theory may allow us to better understand, appreciate and manage the evolving denizens of our planet.

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