Evolutionary Game Theory and Adaptive Dynamics of Continuous Traits

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Abstract

Continuous-trait game theory fills the niche of enabling analytically solvable models of the evolution of biologically realistically complex traits. Game theory provides a mathematical language for understanding evolution by natural selection. Continuous-trait game theory starts with the notion of an evolutionarily stable strategy (ESS) and adds the concept of convergence stability (that the ESS is an evolutionary attractor). With these basic tools in hand, continuous-trait game theory can be easily extended to model evolution under conditions of disruptive selection and speciation, nonequilibrium population dynamics, stochastic environments, coevolution, and more. Many models applying these tools to evolutionary ecology and coevolution have been developed in the past two decades. Going forward we emphasize the communication of the conceptual simplicity and underlying unity of ideas inherent in continuous-trait game theory and the development of new applications to biological questions.

INTRODUCTION

Life is a game. Games have players, strategies, and payoffs. In the evolutionary game, individual organisms are the players, their heritable phenotypes are their strategies, and their per capita growth rates (fitness) are their payoffs. The game happens because the fitness of an individual is simultaneously influenced by its own strategy, the strategies of others, and other features of the abiotic and biotic environment. Evolutionary game theory provides a key mathematical language to understanding natural selection better. Here we review this approach and describe its current applicability within the context of adaptive dynamics, evolutionary stability, and continuous (quantitative) traits.

Evolutionary game theory has advanced greatly from Maynard Smith & Price's (1973) pioneering concept of the evolutionarily stable strategy (ESS). Game theory has become the lingua franca of most concepts in animal behavior (Reeve & Dugatkin 1998) relating to mate choice, breeding strategies, animal contests, social groups, and the evolution of cooperation via forms of reciprocal altruism. Such matrix games as "Hawk-Dove" and "Prisoner's Dilemma" are used to teach many aspects of animal behavior. The 1970s also saw evolutionary game theory applied to continuous traits such as body size and other characteristics that might influence population dynamics within species and between species (Lawlor & Maynard-Smith 1976). Just as in animal social behaviors, evolutionary game theory provides an obvious mathematical language for evolutionary ecology. Evolutionary ecology (broadly defined) explicitly requires the use of conceptual and modeling tools that can make predictions about evolutionary trajectories and outcomes of selection on heritable quantitative traits such as flowering times, age at first reproduction, optimal habitat choice, etc.

Despite advances in the past 20 years, continuous-trait evolutionary game theory remains outside the mainstream of evolutionists, evolutionary ecologists, and their textbooks and courses. Why the disjunction between rapid advances in evolutionary game theory and the slower integration of these advances into the mainstream? First, these new applications fall into what has traditionally been the purview of population and quantitative genetics and must therefore displace a resident approach. Second, the literature on continuous-trait evolutionary game theory can be a confusing Babel of terms, concepts, definitions, and notations. Third, it has been a while (Vincent & Brown 1988) since evolutionary game theory has been reviewed in a succinct and accessible manner. This review aims to address these issues.

HISTORY OF GAME THEORY

Most people (Luce & Raiffa 1957) consider von Neumann the father of game theory (von Neumann & Morgenstern 1944). Primarily interested in economic applications, von Neumann and other pioneers dealt primarily with two-player zero-sum games. In a zero-sum game, one player's gain matches another's loss. Although accurate for some games (for example, casino games), most evolutionary games are likely nonzero.

John Nash (1950) developed the Nash equilibrium in a two-page paper that brought him a Nobel prize. In a Nash solution all players possess a no-regret strategy.

No single player can increase personal payoffs by unilaterally changing strategies. The Nash equilibrium revolutionized game theory. It applied equally well to many-player games, asymmetric games, and non-zero-sum games.

Price, a graduate student of Maynard Smith, introduced two seminal ideas in evolution: evolutionary game theory and the Price equation (Frank 1997) before abandoning the field for other interests, studying Christianity, helping the homeless, and eventually dying homeless himself (Frank 1997). Maynard Smith took it upon himself to publish Price's idea (Maynard Smith & Price 1973) and followed with a seminal book (Maynard-Smith 1982). As Maynard Smith notes, the idea of an ESS had been presaged by the study of sex ratios as a frequency-dependent problem (Fisher 1930, Hamilton 1967). An ESS was defined as a strategy (or set of strategies) that, when common in the population, cannot be invaded by rare alternative strategies—a unilateral change in strategy by one mutant individual will not increase its payoff. Hence, the Nash equilibrium is embedded within the ESS concept (see Bulmer 1994 for a discussion of the similarities and differences), although Maynard Smith developed the idea independently.

Advances continued apace. Auslander et al. (1978) applied the Nash equilibrium to evolutionary games with continuous traits. Several researchers, recognizing the utility of continuous-trait game theory, merged Maynard Smith's evolutionary game theory with more conventional game theory (Brown & Vincent 1987a,b; Roughgarden 1976; Vincent & Brown 1984). In addition, models emerged viewing an ESS as the endpoint of a dynamical evolutionary process (Christiansen 1991; Eshel 1983; Maynard-Smith 1981, 1982; Vincent & Brown 1984, 1987; Vincent et al. 1993). Economists too have realized the power of this evolutionary approach to game theory and incorporated it into their work (Fudenberg & Harris 1992, Gintis 2000, Hofbauer 1996).

Within biology, continuous-trait evolutionary game theory moved in two directions. First, some evolutionary ecologists adapted the tools to solve specific problems of biological interest (**Figure 1**). We examine some of this work at the end of this review. Second, a group of scientists, primarily in continental Europe, advanced the dynamic aspect of evolutionary game theory, renaming the subject adaptive dynamics (Diekmann et al. 1996, Dieckmann & Law 1996, Hofbauer 1996). But with the new insights has come a confusing proliferation of similar and/or identical definitions and terms. As we shall see, the new millennium has continued to refine, advance, and apply the mathematical tools of adaptive dynamics and continuous-trait game theory.

CONTINUOUS-TRAIT GAMES

Continuous-trait games consider strategies that form a mathematical continuum (that is, a section of the real number line), such as. [0,1] or $(-\infty, +\infty)$. This is in contrast to discrete (also called matrix) games where the set of strategies is a finite, unordered list (for example, fight, run, wait). Most traits studied in evolutionary ecology are continuous (or nearly so), such as date of first flowering, time to maturity, an animal's body size, the bill dimensions on a bird, or the allocation of resources to roots, stems, and reproductive tissues on a plant. The developments of matrix and continuous
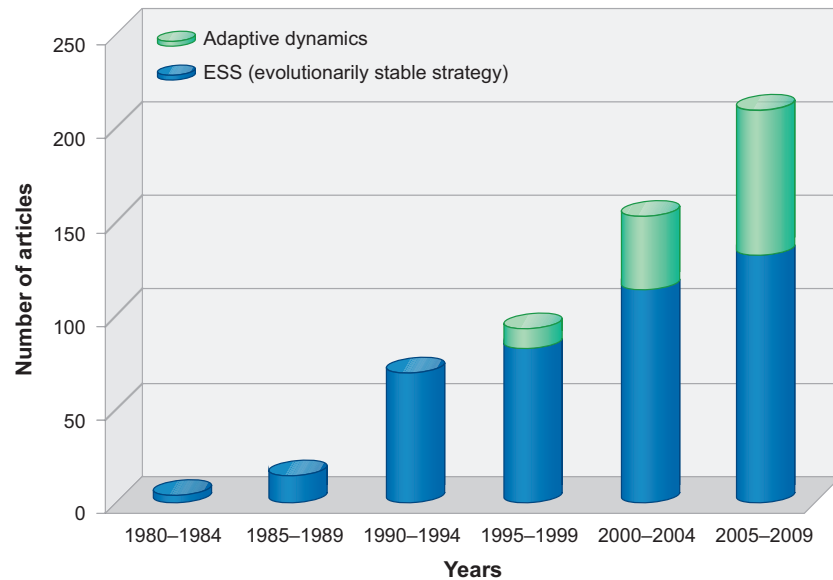
Figure 1

Growth of articles using the terms "ESS" or "Adaptive dynamics" over time. The ISI Web of Science was queried for the number of articles containing either "ESS OR EVOLUTIONARILY STABLE STRATEG*" or "ADAPTIVE DYNAMICS" in their titles, abstracts, or keywords for five year periods. Note that this includes matrix games as well as continuous-trait games owing to the difficulty in separating them out. The years 2005–2009 are estimated based on multiplying the totals for 2005–2006 by 5/2 (probably an underestimate if rates are in fact increasing). The search was limited to 13 mainstream ecology, evolution, and evolutionary ecology journals to avoid medical and engineering terms that also abbreviate to "ESS": *American Naturalist*; *Annual Review of Ecology, Evolution, and Systematics*; *Ecology*; *Ecology Letters*; *Evolution*; *Evolutionary Ecology*; *Evolutionary Ecology Research*; *Journal of Animal Ecology*; *Journal of Ecology*; *Trends in Ecology Evolution*; *Oikos*; *Oecologia*; and *Theoretical Population Biology*. In keeping with our focus on evolutionary ecology, journals primarily focused on behavior were intentionally excluded although they contain a great many additional articles using game theory.

games have followed somewhat independent paths, with various researchers relating the two fields (Day & Taylor 2003, Vincent & Cressman 2000). Although our focus is on continuous traits, the Supplemental Appendix (follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org/**) shows how matrix games are a special case of continuous-trait games.

Basic Tool

The recipe for an evolutionary game begins with an ecological model of population dynamics where we define fitness as per capita growth rate (Crow & Kimura 1970):

$$W(u, U, N) = \frac{1}{N}\frac{dN}{dt}, \qquad\qquad 1.$$

where:

- W denotes fitness. This has a long tradition in population genetics, but many alternative notations have been used in the literature on continuous-trait game theory, including F, G, ρ, σ, etc.

- u denotes the strategy played by the player of interest. Here a strategy is synonymous with some heritable trait such as body size or flowering date.

- U denotes the strategy/phenotype played by the opponent, the resident population.

- N denotes the population size of the resident population.

The Supplemental Appendix provides an example of deriving and developing a continous game: $W(u, U, N)$.

Making fitness a function of various subsets of the $u/U/N$ trio produces a variety of established approaches as special cases. $W(N)$ gives population dynamics. $W(u)$ gives classical optimization theory. $W(u, N)$ gives density-dependent selection, which is known to evolve to the value of u that maximizes the equilibrium value of N (Roughgarden 1979). In contrast, $W(u, U)$ gives frequency dependence without density dependence, a common simplification within game theory. Thus, the u/U pair (frequency dependence) is the *sine qua non* of continuous-trait game theory, giving a twist not found in any earlier approaches. At the cost of losing the strongly mechanistic Mendelian foundations of population genetics, we gain the ability to realistically solve evolutionary models with complex ecologies.

A key innovation of evolutionary game theory involves extending the classical notion of facing a single opponent playing strategy U to facing a population playing strategy U. In Maynard Smith's (1982, p. 23) idea of "playing the field," the individual does not interact in a pair-wise fashion with other individuals; rather the individual faces an opponent that is the population at large. For example, the consequences of flowering date to an individual may be influenced by the interaction between its flowering date (u) and the flowering dates of all of the neighboring plants. In this case we can think of the entire population playing the single strategy U. Under this interpretation we see u as the strategy of a mutant individual or a focal individual, and U is the resident strategy or the strategy found among the N individuals of the population (or N–1 with 1 for the mutant). Even if individuals in the resident population show variation, the playing-the-field approach can still work if the fitness of the target individual is well approximated by considering the average strategy of the resident population, $\bar{U}$, that is, $W(u, \bar{U}, N) \approx W(u, \{U_1, U_2, \ldots\}, N)$. Later we explore extensions where the population has variation in strategy values among individuals that cannot be reduced to the average strategy value.

Not surprisingly, an evolutionary game specified by $W(u, U, N)$ invites three distinct dynamics: the fate of the mutant playing u, changes in the population-wide strategy U, and changes in population size N. We discuss the first dynamic in the next section and the second and third dynamics in the following section.

Evolutionary Stability: Resistance to Invasion

Maynard Smith & Price (1973) considered the fate of a rare mutant or invader (playing strategy u) playing against some resident population (playing U). For evolutionary stability, they suggest "a strategy such that, if most of the members of a population adopt it, there is no 'mutant' strategy that would give higher reproductive fitness." (p. 15) Mathematically, the condition is

$$W(u, U^*) < W(U^*, U^*). \qquad 2.$$

This means that U^* is resistant to invasion by any rare alternative strategy u or in population dynamic terms the population size of the mutant or invader population will decrease owing to lower relative fitness. Mathematically, Equation 2 is equivalent to saying fitness with respect to u takes on a maximum at $u = U^*$ when everyone else is also playing U^* (See **Figure 2**)—U^* is the best response to itself.

Maynard Smith & Price call the strategy U^* an ESS. As recognition grew that the equilibrium identified in Equation 2 is the outcome of only one of three dynamics involved in a game (specifically the fate of a mutant playing u), various researchers gave it more specialized names such as evolutionarily unbeatable strategy (Eshel 1983), δ-stability (Taylor 1989), internal stability (Lessard 1990), evolutionary stability (Christiansen 1991), ESS maximum (Abrams et al. 1993b), and the ESS maximum principle (Vincent & Brown 1988, 2005). Regardless of terminology, it recognizes the same property, namely that an individual cannot increase its fitness by unilaterally changing its strategy.

We need to be careful about two points. First, if W is also a function of N, then we must (*a*) determine the equilibrium population size N^* corresponding to U^*, (*b*) replace Equation 2 with $W(u, U^*, N^*) < W(U^*, U^*, N^*)$, and (*c*) require that $W(U^*, U^*, N^*) = 0$ (that is, no population growth if the resident population is of size N^* and playing U^*). Second, the ESS usually allows $W(u, U^*) = W(U^*, U^*)$ so long as the further condition $W(u, u) < W(U^*, U^*)$ holds, because this will still prevent the rare mutant population from growing (Maynard Smith 1982). This second condition can be relevant for matrix games, but it rarely applies to continuous games.

Not only does Equation 2 give a test for an ESS, but, if we remember calculus, it gives a means to find ESS strategies. Specifically an ESS occurs at maxima of the function W for the variable u, which can be found by requiring

$$\frac{\partial}{\partial u} W(u, U^*) = 0 \qquad 3.$$

and

$$\frac{\partial^2}{\partial u^2} W(u, U^*) < 0 \qquad 4.$$

when evaluated at $u = U = U^*$ (and $N = N^*$ if population dynamics are included). The Supplemental Appendix applies Equations 2–4 to an example of a population choosing between two food patches.

Resistance to invasion is a static concept. It guarantees that a population at (U^*, N^*) can maintain its position against a rare invader, but it says nothing about what would happen if the population starts at (or was perturbed to) a nearby point $U^* + \delta$.
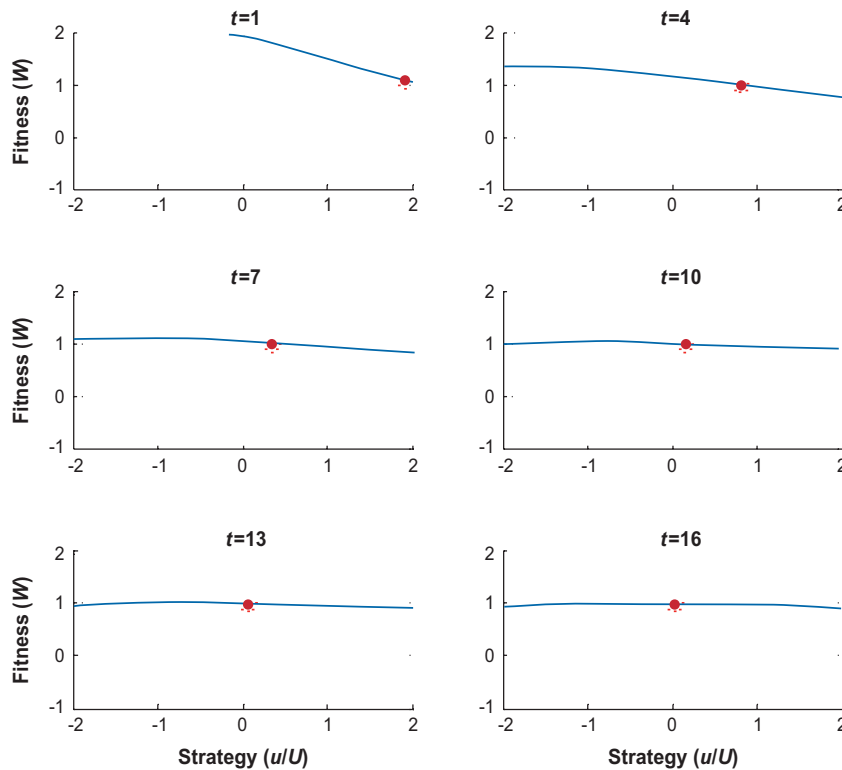
Figure 2

Population moving across adaptive landscape. This figure shows a sequence of snapshots (from $t = 1$ to $t = 16$ with 4 stops in between) of a population evolving in a continuous-trait game model of the Levene model of competiton (Geritz 1998, Levene 1953) (also used in **Figures 3** and **4**). The vertical axis is for fitness, W. The horizontal axis is for the strategy, u/U. The solid line gives the adaptive landscape with the fitness for a mutant of strategy u at each time t when the population is at U_t given by the location of the asterisk. These figures were calculated using the discrete equation for the dynamics of U, that is, Equation 5. Note the following points: (*a*) the population moves up hill, (*b*) the speed of movement is faster up steep slopes and much slower on nearly flat slopes, (*c*) the shape of the adaptive landscape changes as the population moves (U changes), (*d*) this dynamic results in stopping at the top of the hill, (*e*) this stopping point is an equilibrium point which meets the requirements of Equations 3 and 4 [the slope is zero at the evolutionarily stable strategy (ESS), and the second derivative is negative implying a maximum] and is therefore an ESS.

In fact, it is possible that $W(U^*, U^* + \delta) < W(U^* + \delta, U^* + \delta)$ (that is, a point U^* that is resistant to invasion is itself incapable of invading a population with a resident strategy close to but different than U^*; Geritz et al. 2002). Therefore invasion resistance by itself is a poor predictor of the evolutionary dynamics of a whole population. An additional concept is needed known as convergence stability, which we discuss in the next section.

Evolutionary Stability: Adaptive Dynamics and Convergence Stability

To model the evolution of the resident population phenotype *U*, continuous-trait game theory extends Fisher's (1930) *Fundamental Theorem of Natural Selection*, which states that single locus genetic models evolve (change allele frequencies) according to $\Delta p = k \, dw/dp$ where *p* is allele frequency. Visually, the change in gene frequency is in the direction of and proportional to the slope of the adaptive landscape. By extension of the Fundamental Theorem of Natural Selection to evolutionary strategies, the rate of change in the value of a population's strategy, *U*, is proportional to the slope of the adaptive landscape ($\partial W/\partial u$) and in the direction of this fitness gradient (Roughgarden 1983). This leads to a dynamical equation for the change in the resident strategy, U:

$$\Delta U = k \frac{\partial}{\partial u} W(u, U, N) \quad \text{or} \quad U_{t+1} = U_t + k \frac{\partial}{\partial u} W(u_t, U_t, N_t). \qquad 5.$$

The constant of proportionality *k*, is sometimes broken into components involving heritability h^2 and/or additive genetic variance σ^2. If this evolutionary "speed" term is too large, then evolutionary dynamics may become nonequilibrial (particularly for the difference equation dynamic). Equation 5 is sometimes called the canonical equation of adaptive dynamics (Dieckmann & Law 1996). A continuous version is given by

$$\frac{dU}{dt} = k \frac{\partial}{\partial u} W(u, U, N). \qquad 6.$$

Equations 5 and 6 give the second dynamic inherent in $W(u, U, N)$ (changes in *U*).

The third dynamic concerns population size, *N*. By definition of *W* (Equation 1),

$$\frac{dN}{dt} = NW(u, U, N) \quad \text{or in discrete terms} \quad N_{t+1} = N_t + N_t W(u_t, U_t, N_t). \quad 7.$$

Together Equations 5 and 6, and 7 describe the dynamics of the state variables *U* and *N*. For continuous-trait evolutionary game theory, these equations were first suggested without proof by Brown & Vincent (1987a). The 1990s saw rigorous and formal derivations of these equations (Abrams et al. 1993b, Geritz 1998, Metz et al. 1996, Vincent et al. 1993) with perhaps the most detailed being given by Dieckmann & Law (1996). Many different flavors of Equations 5 and 6 exist with different notations, definitions of *k*, and initial assumptions. Fortunately, these evolutionary dynamics are remarkably robust to the slight differences in interpretation.

At least three other approaches to phenotypic evolution have been taken. First, computer simulations of mutating asexual populations can be used when analytical solutions are unavailable (see **Figure 4**). Second, several researchers have shown that learning behavior can lead to strategy dynamics similar to Equation 5. Finally, researchers have explored evolution toward an ESS using population or quantitative genetics models. Although focusing on the purely phenotypic approach to the dynamics, we discuss these three alternative dynamics in the Supplemental Appendix.

It is straightforward to use the dynamical Equations 5 and 6 to identify the convergent stable endpoints of the dynamic (Abrams et al. 1993b, Bulmer 1994, Geritz et al. 1998, Vincent 1990, Vincent et al. 1993). Specifically U^* is an evolutionary endpoint

if Equation 3 holds and if:

$$\frac{\partial^2}{\partial u^2}W(u, U) + \frac{\partial^2}{\partial u \partial U}W(u, U) < 0. \qquad\qquad 8.$$

Or more generally if the dependence of fitness, W, on N is modeled, then a third term is added to the left hand side: $+(\partial^2 W/\partial u \partial N)(\partial N^*/\partial U)$ with $W(u, U^*, N^*) = 0$ (Vincent & Brown 2005). The proliferation of terms referring to the stability of the adaptive dynamic include: continuous evolutionary stability, m-stability, ESS (coopting the earlier meaning) and convergence stability. We will refer to strategies U^* that meet Equation 8 as convergent stable. When U^* is convergent stable it is an evolutionary attractor; populations with U different from U^* will evolve toward U^*. If the opposite of Equation 8 holds (LHS > 0) for a point U^* where Equation 3 holds, then it is an evolutionary repellor; populations just slightly off this point will move further away from it. The Supplemental Appendix provides a worked example of these equations.

The conditions for convergence stability and for resistance to invasion have some important similarities. The first-order conditions of $\partial W/\partial u = 0$ are identical. The second-order condition for convergence stability contains one or two additional terms beyond $\partial^2 W/\partial u^2$. The evaluation of resistance to invasion only involves unilateral changes in an individual's strategy with no changes in the population's strategy or population size. Convergence stability additionally involves the consequences of collective changes in strategy $(\partial^2 W/\partial u \partial U)$ and the effect of the populations strategy on population size, $(\partial^2 W/\partial u \partial N)(\partial N^*/\partial U)$. The term $\partial^2 W/\partial u \partial U = \partial(\partial W/\partial u)/\partial U$ is critical. It captures the idea that the shape of the adaptive landscape $(\partial W/\partial u)$ changes as U changes (see **Figure 2**). This is the famous idea of the adaptive landscape as a rubber sheet that gets stretched as a population moves across it. Wright (1930) was well aware of this effect of frequency dependence and generally avoided it. Continuous-trait game theory, on the contrary, embraces this addition. But it can have profound implications, making evolution short-sighted (Roughgarden 1979)—that is, meaning it evolves in the direction that currently causes the greatest increase of fitness, not necessarily in the direction that will bring it to the highest collective fitness.

Because of the possibility of $\partial^2 W/\partial u \partial U$ being positive or negative, $\partial^2 W/\partial u^2$ can be negative yet Equation 8 can fail, or $\partial^2 W/\partial u^2$ can be positive yet Equation 8 can be true. Thus the two types of evolutionary stability (invasion resistance and convergence stability) do not imply each other.

BESTIARY OF EVOLUTIONARY GAME OUTCOMES

As a consequences of the independence of the two types of stability there are four possible outcomes when evaluating a strategy U^* that satisfies $\partial W/\partial u = 0$. The strategy U^* may exhibit any one of the following outcomes: (*a*) resistant to invasion and convergent stable, (*b*) resistant to invasion and not convergent stable, (*c*) invadable and convergent stable, and (*d*) invadable and not convergent stable (Cohen et al. 1999, Geritz et al. 1998). This creates an exciting bestiary of outcomes.

Understanding the independence of invasion resistance and convergence stability and the resulting four combinations has been the most important advance since the initial formulation of evolutionary games. However, as one can imagine given the half dozen terms for each of two types of stability, there has also been a proliferation of terms for the four outcomes.

We have already given proposed unifying terms for the two types of stability (invasion resistant = meets Equation 2, and convergence stable = meets Equation 8). The four permutations of these two terms suffice to describe all evolutionary outcomes in their full generality. However, we also propose that the four outcomes can be meaningfully further classified into three groups, only two of which are biologically interesting:

ESS: We suggest defining outcome A as the ESS. This means the ESS is an uninvadable fitness maximum and convergent stable. Although Maynard Smith's original definition lacked an appreciation for convergence stability, he fully intended the concept to describe the likely outcome of evolution by natural selection acting on games. We favor updating Maynard Smith's concept for two reasons. First, the term ESS has the greatest cachet in the dictionary of evolutionary ecology—why lose that? Second, fitness maxima that are evolutionary repellors (not convergent stable) will not evolve. Applying the ESS to outcome A follows Maynard Smith's original definition with the necessary addition of convergence stability (which was generally true at a fitness maximum in the discrete games he studiedsee a detailed discussion in the Supplemental Appendix for matrix games).

Branching Point: The term branching point describes outcome C where a strategy is both a fitness minimum and convergent stable. As noted by Brown & Pavlovic (1992) and then extensively developed by Abrams et al. 1993b, Dieckmann & Doebeli 1999, Doebeli & Dieckmann 2000, and Geritz et al. 1997, populations may evolve to these branching points (**Figures 3** and **4**) and then under the right conditions diverge into two separate populations or species with distinct strategies—our topic for the next section.

Repelling points: Outcomes B and D are not convergent stable. Evolution will not move strategies to these repelling points. These points should not be observed in nature. It remains an open question on how these repellors may affect evolution toward ESS and branching points (Doebeli et al. 2004). For example, repelling points may serve to divide basins of attraction between alternate ESSs. Or, like branching points, the existence of repelling points may presage an ESS that contains more than one strategy (see the section entitled "Coalitions and Evolutionary Stable Strategies with Multiple Strategies Played").

An ESS (convergent stable maximum) can be global or local in each of the two types of evolutionary stability. For invasion stability, an ESS can resist only nearby invaders (a local ESS) or all invaders (a global ESS) (Vincent & Brown 2005 prefer to further restrict the usage of ESS to global maxima). Even a global ESS may not be the sole ESS on the landscape—there may be other strategies that are ESSs but they are masked as soon as one of the ESSs is achieved. For convergence stability,
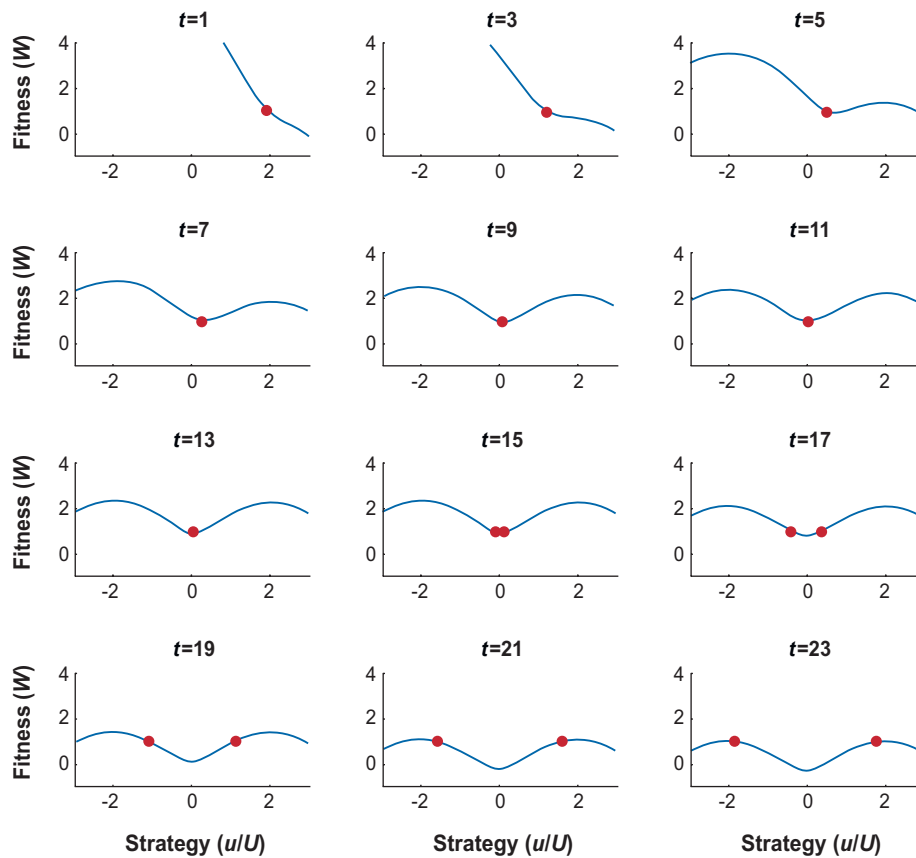
Figure 3

Evolution toward minimum fitness. This is the same model of competition used in **Figure 2**, but the parameter for niche width has been decreased to allow two distinct fitness peaks to emerge. This example shows how evolutionarily stable strategy (ESS) dynamics can in fact cause a population to evolve toward a fitness minimum. This depends critically on the fact that the landscape changes shape as the population evolves. The basic effect is that the landscape changes shape faster than the population moves. Just before time $t = 15$ the population was split into two subpopulations starting just slightly to either side of the fitness minimum. With two populations, the populations are now able to evolve apart toward the two fitness maxima (ESSs). This is an example of a branching point. This is also an example where a coalition of two is able to invade an equilibrium that is uninvadable by any coalition of one.

all possible starting strategies can converge to the ESS (globally convergent) or only some subset of initial strategies (called the basin of attraction) will evolve to the ESS (locally convergent). A globally convergent landscape can have only one ESS whereas systems with multiple ESSs (necessarily only locally convergent) will have a distinct basin of attraction associated with each ESS.

With these local and global properties applied to each outcome of invadability and convergence stability, the bestiary of possibilities grows! For instance, the ESS may
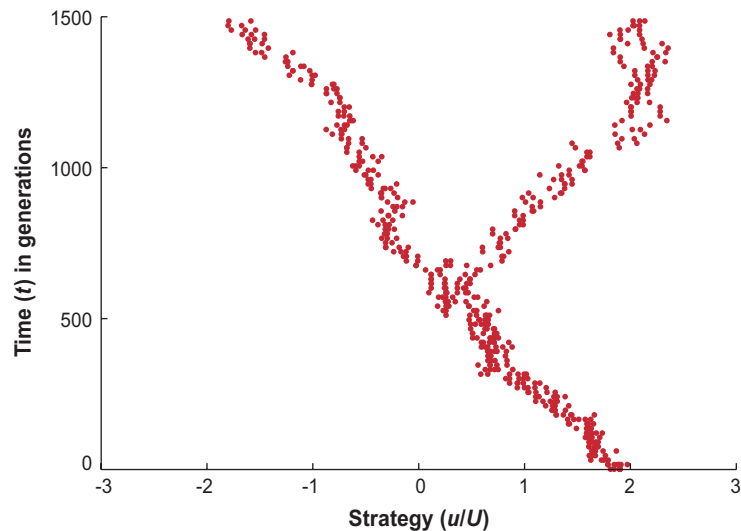
Figure 4

Individual-based models and branching points. This figure is an example of using a computer simulation of an individual-based model (IBM) of a population reproducing asexually with occasional mutation (see Supplemental Appendix). In this simulation the same game as in **Figure 3** is modeled. The result is very similar—the population evolves to the branching point at $U = 0$, then splits into two populations (a coalition) moving to the two peaks near $+2$ and -2. The main difference is that the population already had a spread of phenotypes and did not require the specific intervention of adding a second population at the branching point. There is considerable debate about whether this branching will occur when the organism reproduces sexually.

be globally convergent stable but not a global maximum. Once this ESS has evolved, a distant strategy can invade. But once this distant strategy starts to become common it either (*a*) moves toward U^* and merges back into U^* or (*b*) goes extinct. This is known as the resident strikes back scenario (Dieckmann et al. 1999). This outcome requires weird mathematical conditions and it may or may not be biologically likely (Geritz et al. 2002).

This brings us to the current frontier of evolutionary game theory where strategy dynamics lead to a dizzying array of outcomes. When population dynamics are overlaid on the strategy dynamics, the possibilities become Byzantine. Geritz et al. (1999) point out that this diversity of outcomes occurs because of interactions between the two stability properties of resistance to invasion and convergence stability. A single model (Geritz et al. 1999) exhibited at least five different types of bifurcations, as follows:

1. Global ESS becomes local ESS with no other equilibria appearing,

2. Repellor and branching point appear simultaneously (with branching point adding a strategy or causing extinction),

3. ESS and repellor collide and annihilate each other,

4. Global ESS becomes local ESS simultaneously with appearance of branching point and repellor, and

5. Branching point leads to a coalition of two strategies, one of whose equilibria is a continuation of the local ESS.

The exploration of bifurcations in adaptive dynamic systems remains perhaps the most important theoretical topic left to pursue in continuous-trait game theory.

ADAPTIVE SPECIATION AND BRANCHING POINTS

Branching points are evolutionary attractors that are fitness minima (that is, Equation 2 is false but Equation 8 is true). In some models, the evolution of the resident population strategy U can evolve uphill along the adaptive landscape yet come to rest at a minimum. This occurs because the adaptive landscape changes even as the strategy moves along it (see **Figure 3** for an example of this counterintuitive dynamic). When the population is at strategy $U^* - \delta$ ($\delta > 0$ here) the, landscape takes on a positive slope. At $U^* + \delta$ the landscape takes on a negative slope; but when the population plays exactly U^*, the signs reverse leaving U^* at a minimum. Even if the system starts with two evolving species with strategies that are close together but distinct, the process of branching occurs. At first, the two evolving populations may climb the same slope toward what would be the branch point, but as the strategies approach the minimum, the position of the minimum itself moves to a point between the species. The species do not need to cross the valley of the landscape, rather the valley crosses under them.

Multiple fates of these two separately evolving populations can be imagined:

1. Both populations continue to evolve and move toward something like an ESS, they remain two populations with distinct strategies—the ESS may contain more than one distinct strategy.

2. One or both populations diverge to strategies that are themselves branching points, permitting the process of strategy diversification to continue as an adaptive radiation.

3. One population evolves toward its own extinction whereas the other moves away from the branching point toward an ESS.

4. Both populations become extinct.

Outcomes 1 and 2 raise two questions: Can we describe these branching, separately evolving populations as species? And how do we define an ESS with two resident strategies instead of one?

Outcome 3 might seem counterintuitive: How can a population evolve in the direction of increasing fitness until it goes extinct? In fact, several biologically realistic examples of this have been identified (Geritz et al. 1999, 2002). Runaway selection provides one example where some trait of the population becomes ever more extreme owing to evolutionary forces, but the equilibrium population size for the more extreme trait becomes progressively smaller until extinction occurs. Thus we need an adjective to describe different types of branching points. We propose calling outcomes 1 and 2 (two or more permanently evolving populations) coalition branching

points for reasons that are made clear two sections below. We propose calling outcome 3 extinction branching points. Ferrière and coworkers called outcome 4 evolutionary suicide (Ferrière 2000), although this may require mathematically precise and biologically unrealistic conditions (Geritz et al. 2002).

Speciation: Do Branching Points Really Branch?

The identification of branching points may lead to major advances in the studies of sympatric speciation and adaptive radiations. That these convergent stable minima are a real phenomenon of game theory is demonstrable fact. What they mean in nature is an open and exciting empirical question. Are there species in nature with strategies that reside at one of these minima? There has been debate for (Cohen et al. 1999, 2001) and against (Abrams 2001, Waxman & Gavrilets 2005) the relevance of branching points to natural systems.

Early models and tests of sympatric speciation (Maynard Smith 1966, Thoday & Gibson 1962) used disruptive selection as the driving mechanism of speciation. As shown in most evolution textbooks, this disruptive selection explicitly or implicitly assumes that the resident phenotype of the population is at a minimum of the adaptive landscape. But how did the population's phenotype get to this point of disruptive selection in the first place?

Evolutionary game theory and the phenomenon of branching points (convergent stable minima) resolve these problems with nongame theoretic models of sympatric speciation. Natural selection evolving up the fitness gradient can itself arrive at the minimum of frequency-dependent adaptive landscapes. When the number of resident strategies is below that of the ESS (see the next section below on Coalitions and Evolutionary Stable Strategies with Multiple Strategies Played), natural selection may drive the strategy to the branching point, exert disruptive selection, and permit speciation. Rosenzweig (1978) anticipated some of these properties of frequency- and density-dependent adaptive landscapes in what he called competitive speciation.

Current modeling and conceptual research addresses the question of how branching points can permit speciation. With asexually reproducing organisms branching occurs easily (**Figure 4** and Geritz & Kisdi 2000). But sexual reproduction creates a blending or interbreeding between separating populations that may preclude splitting the population into subpopulations with distinct resident strategies (Tregenza & Butlin 1999). This fact is captured in the discontinuous jump that was required between time steps 13 and 15 in **Figure 3**—the researcher who conducted the computer simulations had to arbitrarily introduce two populations as the progenitor population approached the branching point.

Several mechanisms may allow speciation even under sexual reproduction. First, species may assortatively mate on the trait that is subject to disruptive selection. This is conceivable, for example, for body size. In fact, if the species persists at a branching point, selection strongly favors assortative mating! Second, a marker trait or sexually selected trait such as throat color may become linked to the trait under disruptive selection and allow assortative mating on the marker trait. The assortative mating becomes adaptive because of the lesser fitness of intermediate

types (Dieckmann & Doebeli 1999, Doebeli & Dieckmann 2000, Geritz & Kisdi 2000, Kisdi & Geritz 1999). Third, and perhaps most likely, these traits may cause organisms to be more commonly found at sites (host plants, elevations, microhabitat) to which they are most adapted (either through active choice by the organism or by Darwinian selection), and the spatial separation correlated with the trait leads to assortative mating as a byproduct of proximity (Doebeli & Dieckmann 2003). It is important to note that these four modes of speciation (asexual and the three assortative mating mechanisms) not only are not unique to adaptive dynamics but were developed first and most extensively elsewhere (Kondrashov 1986, Kondrashov & Kondrashov 1999, Rosenzweig 1978).

The novel and wonderful contribution of adaptive dynamics to sympatric speci- ation is in showing how the disruptive selection comes about. Prior to game theory, disruptive selection was often considered somewhat pathological or a chance event. But with the inclusion of density and frequency dependence into standard models of population dynamics, we see disruptive selection occurring easily in the form of branching points. These branching points emerge as a very common and widespread property of continuous-trait games.

Coalitions and Evolutionary Stable Strategies with Multiple Strategies PlayedEvolutionarily Stable Strategies

In matrix game theory it was recognized that a single strategy may not be an ESS. For instance, in a Hawk-Dove game, the strategy Dove may have a higher payoff than Hawk in an all-Hawk world and vice-versa for Hawk having a higher payoff in an all-Dove world. Consequently, the two strategies coexist. Just like matrix games, the ESS for continuous-trait evolutionary games may possess a coalition of coexisting strategies. The existence of branching points in models suggests that the model may have an ESS coalition with two or more strategies.

The ESS concept extends nicely to cover ESS coalitions of n populations, playing strategies $U_1, U_2, \ldots U_n$. The extension of notation is straight forward:

$$(1/N_i)(dN_i/dt) = W(u, U_1, U_2, \ldots, U_n, N_1, N_2, \ldots N_3) = W(u, \mathbf{U}, \mathbf{N}) \quad \text{for} \quad u = U_i$$
$$9.$$

where the boldfaced $\mathbf{U}$ and $\mathbf{N}$ represent vectors of the resident strategies and their population sizes for $i = 1, \ldots, n$. Brown & Vincent first developed the idea of an ESS coalition of more than one strategy, referring to Equation 9 as the fitness generating function (using G instead of W). Although not explicit, they considered the ESS (given Equations 10 and 11 below) to be both resistant to invasion and convergent stable (Brown & Vincent 1987b; Vincent & Brown 1984, 1988; Vincent et al. 1996). With the discovery of branching points, the ESS coalition has become an important and necessary extension. and others have readily adopted it (Geritz et al. 1998, 1999). By setting $u = U_i$ in the function, one generates the fitness function for the population using strategy i.

The necessary conditions for $\mathbf{U}^*$ to be resistant to invasion represent a straight- forward extension of Equations 2 and 3 (Brown & Vincent 1987b; Vincent & Brown

1984, 1988; Vincent et al. 1996):

$$\frac{\partial}{\partial u} W(u, U_1, U_2, \ldots, U_n, N_1, \ldots, N_n) = 0 \quad \text{for} u = U_i \quad \text{for each} \quad i \qquad 10.$$

and

$$\frac{\partial^2}{\partial u^2} W(u, U_1, U_2, \ldots, U_n, N_1, \ldots, N_n) < 0 \quad \text{for} \quad u = U_i \quad \text{for each} \quad i, \qquad 11.$$

where each population of the coalition must exist at positive population size: $N^*_i > 0$. Resistance to invasion requires that each strategy of the ESS reside on a separate peak of the adaptive landscape and that each of these peaks have the same fitness, which is zero at $\mathbf{N}^*$: $W(u, \mathbf{U}^*, \mathbf{N}^*) \leq W(U_i, \mathbf{U}, \mathbf{N}) = 0$ for all $i = 1, \ldots n$. Changes in N_is balance the adaptive landscape so that all strategies of the coalition reside on peaks of equal fitness.

The concept of convergence stability also remains the same for a coalition with just one strategy. The necessary first order condition remains the same as Equation 3, but the second order conditions analogous to Equation 8 become onerous and quite intractable above a coalition of three or more strategies (Cohen et al. 1999, Geritz et al. 1998). But the idea continues to be that $\mathbf{U}^*$ is convergent stable if strategy dynamics will return the populations' strategies to $\mathbf{U}^*$ following a perturbation of δ_i to one or all of the strategies of the coalition (where $U_i = U^*_i + \delta_i$ refers to a perturbation of strategy i). Graphical methods using invasion cones for analyzing 2-coalitions often work better (Geritz et al. 1998, Matessi & Di Pasquale 1996), and other times simply verifying the uninvadability of an n-coalition is adequate (for example, Brown 1990a). Generally the convergence stability of a candidate $\mathbf{U}^*$ is evaluated using adaptive dynamics to see what happens to coalitions with starting conditions close to $\mathbf{U}^*$. Additional work is continuing in this area. There are currently no general results indicating when a model or circumstance will yield an ESS with specifically n-strategies.

Recently, Cohen (2003) has introduced a new approach that is analytically more difficult but biologically more realistic than the idea of a coalition. Rather than a point or set of points along the strategy continuum, Cohen models the evolution of a probability distribution on the strategy continuum. Thus, the resident population could play strategies that are, for example, normally distributed along the continuum. When the mutant "plays the field," the field is then this probability distribution. This has much in common with the use of quantitative genetics to model phenotypic evolution (Abrams et al. 1993a). Although an ongoing and exciting development, the approach remains rather intractable.

EXPANDING THE DOMAIN OF EVOLUTIONARY GAME THEORY

Thus far, we have developed the machinery for predicting phenotypic evolution of a single trait for deterministic systems with stable and fast population dynamics. Can this machinery be expanded to cover more complicated situations? We explore some of these extensions.

Density Dependence and Nonequilibrium Population Dynamics

So far we have largely ignored the dynamics of population size, N. The justification for doing this is a fast/slow argument—evolution proceeds slowly relative to population dynamics. Hence, once can assume that strategy dynamics occur mostly when the populations are at or near N^*.

Of course, this may not always hold. First, strategy dynamics may be fast (for example, selection strong enough) and with a comparable time scale to population dynamics (Yoshida et al. 2003). Second, population dynamics may exhibit oscillations or even chaos. Both may happen for traits associated with predator-prey interactions. Predator/prey models frequently show cyclical dynamics, and the evolution of predation traits may also cycle as the evolutionary responses oscillate with the population dynamics (Abrams & Matsuda 1997, Dieckmann et al. 1995).

When evolution is almost as fast as population dynamics, or if the population dynamics do not have a stable point equilibrium, then we have two modeling choices. We can simulate the system using Equations 5 and 7, or we can use an analytical solution. The analytical solution looks at long-term fitness using the idea of a Lyapunov exponent (Caswell 2001, p. 542 and 561; Ferrière & Gatto 1995, Rand et al. 1994). A Lyapunov exponent can be thought of as the log geometric mean of fitness.

$$
\begin{aligned}
W_{longterm}(u, U, N) &= [\log |W(u, U_1, N_1)W(u, U_2, N_2)\ldots W(u, U_T, N_T)|]^{1/T} \\
&= 1/T \, \Sigma_i \, \log |W(u, U_i, N_i)|
\end{aligned}
\qquad 12.
$$

So if the population dynamics follow a five-cycle, then we geometrically average the fitness of the invading phenotype u, across the five different population sizes N_i in the cycle and the corresponding population strategies U_i. The geometric average is used because population growth is multiplicative ($N_T = W_T \ldots W_2 W_1 N_0$), whereas the log is mathematically convenient. If chaotic rather than cyclic dynamics occur, then we must take the limit as $T \to \infty$. When using Lyapunov exponents, modelers generally favor using a discrete population dynamic based on $N_{t+1} = N_t W(u, U_t, N_t)$, where equilibrium occurs when $W = 1$.

With Lyapunov exponents we say that if $W_{longterm}(U, U) > W_{longterm}(u, U)$ for all (nearby) u (that is, U is a global or local maximum in $W_{longterm}$), then U is an ESS under nonequilibrium dynamics. Although a logical extension of the idea that an ESS is a fitness maximum, it is now only true in the long-term. It is possible for an invading mutant to have negative fitness in one half of a population cycle, positive fitness in the other half, but overall a positive Lyapunov exponent. If the mutant begins its invasion in the half of the cycle where fitness is negative, then it will fail, but in the long-term such a mutant should invade if repeated attempts occur. Thus, we can achieve a strong analytic result (using Lyapunov exponents), but it holds true only in a long-term, averaged-across-many-replicates sense. Finally, the property of convergence stability remains poorly understood for nonequilibrium populations and/or fast evolutionary dynamics.

Stochastic Environments

We have developed the ESS concept as a deterministic process, but the world experienced by organisms is inherently stochastic. Temperature, precipitation, and other factors fluctuate randomly. Many interesting questions in evolutionary ecology derive from such stochasticities (Cohen 1966, Roff 2002).

Stochasticity has the potential to change the evolutionary outcome when the model has multiple ESSs by stochastically bouncing from one basin of evolutionary attraction to another. We can define an uninvadable strategy in a stochastic environment result by using mathematics similar to that for nonequilibrium population dynamics. We denote environmental conditions (for example, temperature) here by a little e and subscript it by t for time to suggest that this takes on varying values over time according to the probability distribution $\mathcal{E}$. We take the same concept of a Lyapunov exponent, except here we average not over the sequence of population sizes, N_t, but over the environmental states, giving:

$$W_{stochastic}(u, U, \mathcal{E}) = E_{\mathcal{E}}\{\log(u, U, \mathcal{E})\} = 1/T \, \Sigma_t \, \log W(u, U, e_t), \qquad 13.$$

where $E_{\mathcal{E}}$ denotes taking the expectation with respect to $\mathcal{E}$. In practice this can be done by taking a simple average over a number of samples from $\mathcal{E}$. In more advanced models it is important to know not just $\mathcal{E}$, but the autocorrelation structure across time (for example, do good years tend to follow good years) (Tuljapurkar 1990, Tuljapurkar & Orzack 1980).

Equation 13 suggests that $W_{stochastic}$ should parallel $W_{longterm}$, and indeed similar issues arise. We can make a weak statement using $W_{stochastic}$ as an invasion exponent (Metz et al. 1992, Rand et al. 1994) and determine which phenotypes can invade against all other phenotypes. This identifies a coalition of phenotypes likely to be present and is sometimes called an evolutionarily stable combination (ESC) (Cohen & Levin 1991, Ellner & Hairston 1994, Ludwig & Levin 1991). This avoids making a strong statement about the one phenotype to win. A stronger statement about a local or global maximum of $W_{stochastic}$ (a stochastic ESS) emerges by looking for a fitness maximum in $W_{stochastic}$, but declaring a precise ESS strategy can be misleading when the biological reality will likely involve a cloud of indistinguishable strategies around this ESS. Furthermore, as before, the convergence stability of systems using Lyapunov exponents for either fluctuating populations or environments remains an unsolved problem.

Structured Populations

Thus far we have ignored age or stage structure. In reality populations are subdivided by age, size, and spatial structure, and there may be evolutionary strategies associated with different stages or ages, or a given strategy may influence different stages differently. Matrix models can examine the population dynamics of structured populations (Caswell 2001). The ESS machinery applies to matrix models of population dynamics. The dominant eigenvalue of the matrix determines the long-term behavior of the population dynamics. As an evolutionary game, we simply equate fitness

$W(u, U, N)$ to the dominant eigenvalue (Caswell 2001; Doebeli & Ruxton 1997; Vincent & Brown 2001, 2005) $W(u, U, N) = \lambda(u, U, N)$, and apply the standard conditions for seeking resistance to invasion (maxima of W is an ESS, etc). The conditions for convergence stability also remain the same with the caveat that one assumes that a stable age or stage distribution is established quickly. Like the assumption of fast population dynamics to a stable equilibrium, we now assume fast dynamics on maintaining and adjusting the stable stage distribution.

Structured (matrix) populations in a stochastic or nonequilibrium environment can also be studied through a combination of Lyapunov values and dominant eigenvalues. Although conceptually straightforward, the modeling begins to invoke complicated mathematical machinery (Caswell 2001; Doebeli & Ruxton 1997; Tuljapurkar 1990, 1997; Tuljapurkar & Orzack 1980). Furthermore, the actual time distribution of population sizes may result from an interaction of resident strategies and stochasticity. For such a case, one must use a simulation to produce a distribution of states and then examine the best response to this distribution (Schmidt et al. 2000).

Multiple Traits

One often studies the evolution of two traits simultaneously. Equations 2–4 and 6–8 have exact analogues for the evolution of multiple traits, but the terms are now vectors and matrices instead of scalars. For instance, a strategy, u or U, is now a vector where each element represents one trait. Details are in Leimar (2005). Most importantly, the scalar k from Equation 6 turns into a matrix. If the two traits are independent, then k is diagonal, and it can be shown that the traits can be modeled separately. However it is common for traits to covary owing to linkage, epistasis, or other covariances. For example, life history traits such as age at maturity, body size, fecundity, and lifespan all have well-known positive and negative correlations (Roff 2002).

When traits do covary, k is no longer diagonal. Strategy dynamics now occur on a two-dimensional landscape with each trait forming one axis, and maxima look like hills. In a two-dimensional landscape, the strategy vector has many possible directions for moving uphill. The exact path up the landscape is determined by the sequence of mutations, which are in turn constrained by the covariance of the traits (Dieckmann & Law 1996, Leimar 2005, Matessi & Jayakar 1976). This outcome is already known in quantitative genetics (Lande 1979). In unusual circumstances, such as when there are two close peaks with a saddle (pass) between them, the indirect route of adaptive dynamics can cause evolution to leave the basin of attraction of one peak and evolve to the other peak (Leimar 2005, Matessi & Jayakar 1976). Leimar (2001) refers to this change in evolutionary outcome resulting from the sequence of mutations as a Darwinian demon, but in practice the conditions in which this can happen may be quite unlikely (Leimar 2005). A promising new approach to the evolution of multiple traits extends Levins' visual fitness set diagrams (Levins 1968) to the frequency-dependent scenario (de Mazancourt & Dieckmann 2004).

Regardless of whether the two traits covary, evolving in two-space offers a new feature. Instead of just having attractors and repellors, equilibrium points can now be saddle points, attracting in some directions in trait space and repelling in others.

Although saddle points are unstable as an evolutionary endpoint, evolution can spend large amounts of time flying by the saddle points, giving them a strong structuring role in the dynamics (Cushing et al. 2002).

Under vector-valued strategies the ESS concept likely remains unchanged. Evolutionary branching points can still occur and behave as sources of speciation. But, now we have the opportunity for the vector of traits to become coadapted within the organism. In this way, many of the covariances seen across species in certain traits (bill length and bill depth in many birds) may be the result of coadaptation and not genetic constraints.

Multiple Species and Coevolution

Continuous-trait game theory provides an excellent tool to model the coevolution of species. In fact, coevolution is really just a special case of the multitrait case described above where the traits are independent of each other (that is, the covariance matrix, k, is diagonal) because they are different species.

For example, for a two-species system with one trait coevolving in each species we have:

$$W_1(u, U, V, N, M) \quad \text{and} \quad W_2(v, U, V, N, M), \qquad 14.$$

where the fitness function is subscripted by species and may take quite different forms in an asymmetric coevolution model such as predator/prey. As always, we explore the fitness of a mutant of species 1 playing the strategy u against a population of species 1 playing the strategy U and the population of species 2 playing the strategy V. Population sizes of N and M refer to species 1 and species 2, respectively. (Note that any rare mutants in species 2 playing strategy v are assumed to have no effect on a rare mutant of species 1 playing strategy u.) Likewise we explore the fitness of a mutant in species 2 playing strategy v against the same context.

The model can easily be extended to more than two species. For example, $W_1(u_i, \mathbf{U}, \mathbf{V}, \mathbf{N}, \mathbf{M})$, where $\mathbf{U}$ and $\mathbf{N}$ are vectors, gives the strategies and population sizes for different prey species, while $W_2(v, \mathbf{U}, \mathbf{V}, \mathbf{N}, \mathbf{M})$ may be the predator's fitness function, where elements of $\mathbf{V}$ and $\mathbf{M}$ represent different predator species. Note that all predators share the same basic fitness function, W_2, but there is one equation for each u_i and v_i (an invading mutant for each species). This is sometimes referred to as a fitness generating function (Brown & Vincent 1992).

Evolution is now occurring along several adaptive landscapes, one for each species. The strategies and population sizes of all species may influence the shape of each species' adaptive landscape. The conditions for resistance to invasion remain unchanged, $\mathbf{U}^*$ and $\mathbf{V}^*$ must simultaneously take on maxima of their respective landscapes and, at equilibrium populations sizes, these maxima will yield 0 fitness. The concept of convergence stability remains the same but the conditions are quite unwieldy and have yet to be fully described with more than two species. The ESSs can still be defined as coalitions of strategies that are convergent stable and resistant to invasion but can now involve multiple species of prey and predators. The prey and/or predator's adaptive dynamics may lead to evolutionary branching, nonequilibrial

evolutionary dynamics, and local maxima (Dieckmann et al. 1995). Such a model allows for coevolution both within and between the predator and prey species.

APPLICATIONS OF CONTINUOUS-TRAIT GAME THEORY

It is impossible to summarize in a single review article all biological problems that have been studied using continuous-trait games (see **Figure 1**). Here is a very brief summary. Broadly speaking, biological applications of continuous-trait game theory fall into two categories, models of evolution of a single species (evolutionary ecology) and models of evolution between two species (coevolution).

Evolutionary Ecology

In 1983 three nearly simultaneous papers (Bulmer 1983, Iwasa et al. 1983, Parker & Courntey 1983) used ESS models to explain the well-known phenomenon of protandry in insects (males emerge before the females). These models suggested not only that early emergence should occur but that there should be an abrupt drop-off in male emergence before the end of female emergence. Additional predictions include: environmental stochasticity should lead to increased variation in emergence time under all conditions and tracking of the female emergence times if this is predictable (Iwasa & Haccou 1994); a variety of modifications occur in divoltine populations (Wiklund et al. 1992); arrival order of migratory birds should depend on individual condition (Kokko 1999); and if disturbances (for example, late freezes) influence emergence times, then optimal emergence strategies depend on the spatial scales of disturbance and population regulation (Iwasa & Levin 1995).

Cohen (1966) studied dormancy in annual plants (seed banks) without density dependence and showed that dormancy (partial germination) was optimal in a stochastically varying environment. Seger & Brockman (1987) pointed out that this same line of thinking applies to diapausing insects and named this argument bet-hedging. In the mid-1980s several researchers (Bulmer 1984; Ellner 1985a,b; Goodman 1984) nearly simultaneously applied game theory to identify ESS solutions showing that the inclusion of density and frequency dependence caused an increase in the optimal dormancy fraction. Tuljapurkar & Istock (1993) studied the effect of environmental harshness and temporal weather autocorrelations on diapausing. Simultaneous temporal stochasticity and deterministic spatial heterogeneity (with limited dispersal) can lead to branching points with the coexistence of multiple germination strategies (Mathias & Kisdi 2002).

At this writing (February 2007), over 95 papers have analyzed the evolution of dispersal using a game theoretic approach. Game theory can explicitly allow for density and frequency dependence and/or environmental variation. Several researchers (Comins et al. 1980, Motro 1982, 1983) suggested that dispersal would be an ESS to avoid kin competition. Kin selection in ESS models is discussed generally, with an example based on dispersal, by Taylor & Frank (1996). Levin et al. (1984) showed that stochastic spatial heterogeneity could also make dispersal an ESS, a conclusion expanded in several directions (Lemel et al. 1997, Mathias et al. 2001). Several

researchers have explored how nonequilibrium population dynamics (for example, chaotic) favor dispersal (Doebeli & Ruxton 1997, Gyllenberg & Metz 2001, Holt & McPeek 1996, Parvinen 1999). A number of researchers also explore local (seed) dispersal and possible trade-offs on seed size and/or competition (Ezoe 1998, Lavorel et al. 1994, Levin & Muller-Landau 2000, Winkler & Fischer 1999). Dispersal in a metapopulation (Gyllenberg et al. 2002) can evolve to the point where the species drives itself extinct. Evolution of dispersal can lead to branching points and dimorphisms in dispersal strategies (Doebeli & Ruxton 1997, Mathias et al. 2001) or to phenotypically plastic reaction norms (Ezoe & Iwasa 1997). The link between dispersal and various other life history strategies such as age of reproduction (Ronce et al. 2000) and brood size (Kisdi 2004) has been explored. Other analyses have identified the ESS strategy for migration versus overwintering (Kaitala et al. 1993) and joining or leaving social groups (Kokko & Johnstone 1999, Stephens et al. 2005).

The evolution of seed size versus seed number (or any offspring number versus offspring quality trade-off) is also amenable to ESS modeling. As with dormancy and dispersal, optimization models make one prediction, but ESS models that include density dependence and/or environmental variation make different predictions. Specifically, the Smith-Fretwell model (1974) predicts an intermediate seed size, but empirical observations show considerable variation in seed size within a single parent. Using game theory one can introduce a variety of factors that predict variation in seed size within a single parent, including the introduction of a stochastic environment (Yoshimura & Clark 1991), the assumption of asymmetric competition favoring larger seeds (Geritz 1995, Geritz et al. 1998), and the existence of size-selective predators (Geritz 1998). As already discussed, seed size is often correlated with dispersal ability, resulting in several ESS analyses of the trade-off (Ezoe 1998, Levin & Muller-Landau 2000). The evolution of optimal body size at maturity in animals is similarly enhanced by the use of game theory to include density dependence and/or stochastic environments (Lytle 2001). The existence of asymmetric competition also explains allocation to inefficient support structures required to achieve large body sizes (for example, woody growth in trees) and may explain the mixture of body sizes observed within a community (Falster & Westoby 2003).

Venable & Brown (1988, 1993) presented a synthesis that ties the last three paragraphs together. Seed size, dormancy, and dispersal are all strategies that reduce risk from temporal variability in three factors: environmental stochasticity, crowding, and sibling competition. They showed that a change in one trait leads to a change in the optimum of the others, ultimately leading to the existence of trade-offs resulting from bet-hedging.

Habitat choice and the evolution of specialists and generalists are also frequently analyzed using game theory because choice of habitat clearly depends on what habitats other individuals are choosing. Although Fretwell never mentioned game theory, his concept of an ideal free distribution or IFD (Fretwell 1972, Fretwell & Lucas 1969) is a game, as shown by the worked example in the Supplemental Appendix. Rosenzweig and Abramsky have done extensive theoretical and field work on habitat choice (Abramsky et al. 1991, 1997; Rosenzweig 1981, 1987). Joel Brown has extended this work in an explicitly game theoretic context (1988, 1990b, 1992, 1999).

Brew (1982) used game theory to extend this work from discrete patches to a spatial continuum. It has also become clear that the game of habitat selection can lead to the evolution of both generalists and specialists, and to the coexistence of multiple species (Brown 1998, Kisdi 2002, Schmidt et al. 2000).

Coevolution

Game theory becomes a tool for modeling coevolution and the evolution of niches once different strategies of an ESS coalition represent different species, and branching points provide opportunities for speciation. For modeling the coevolution of competitors, Lotka-Volterra competition equations, consumer-resource dynamics, and Levene hard selection and plant growth models have been used as the ecological starting point for W (Apaloo et al. 2005, Brown & Vincent 1987a, Cohen et al. 1999, Cressman & Garay 2003, Flaxman & Reeve 2006, Geritz et al. 1998, Rees & Westoby 1997, Vincent et al. 1996). As we have already seen (**Figures 3** and **4**), competition can lead to branching points and coalitions with multiple species, in some cases through repeated cycles of additional branching (that is, coexistence of many species). But although branching points can be sufficient to achieve the ESS community of n-species, the process in Lotka-Volterra models often proceeds nicely to n–1 species, but then an insurmountable valley emerges separating an occupied peak from an unoccupied peak of even higher fitness (Vincent & Brown 2005). Even when the niche space is continuous, game theory models of competition generally result in a finite number of distinct species with strategies spread out along the niche axis (Mitchell 2000). This result parallels the idea of limiting similarity (MacArthur 1967), but the ESS generally supports fewer species with wider niches than possible under strict nonevolutionary niche packing.

Models of predator-prey coevolution require at least two independent fitness functions built around an ecological model for the prey and another for the predator (Abrams & Matsuda 1997, Bowers et al. 2003, Brown & Vincent 1992, Dieckmann et al. 1995). Any standard model of predator-prey population dynamics can be fashioned into an evolutionary game where the prey have a strategy or vector of strategies influencing resource acquisition, competition, and susceptibility to predation. The predators possess a strategy that influences their ability to catch prey, which is simultaneously influenced by the prey's strategy. These models reveal several important outcomes. First, predator-prey coevolution frequently produces branching points that enhance the number of prey and/or predator species in the ESS (Brown & Vincent 1992, Kisdi 2006). Second, a predator species may be evolutionarily keystone and necessary for promoting the presence of additional prey species within the ESS (but once the prey species has evolved, the predator species may not still be necessary for prey coexistence). Third, sometimes when the number of predator species and prey species is well below the numbers of the coalition ESS, the strategy dynamics will result in perpetual cycling where the prey strategy evolves away from the predator and the predator's strategy chases after it. Or the system may self-annihilate as the predator strategy chases the prey strategy to such extreme values that the prey evolves to extinction.

Coevolution of mutualisms offers a new frontier for evolutionary game theory (De Mazancourt et al. 2005). Like other forms of species interaction, frequency dependence can create ESS coalitions with many coexisting species (Bever 1999). But a number of issues unique to mutualism are emerging. Mutualisms face a Prisoner's Dilemma-like game in which taking from the partner but not giving is the optimal strategy. A variety of mechanisms have been identified that allow a mutualism to coevolve (McGill 2005). The coevolution of mutualisms can in turn affect the evolution of other life history traits (like root:shoot ratio) (Geritz et al. 2006).

Despite the literally hundreds of papers already published (**Figure 1**), continuous-trait game theory is only just beginning to tap into its potential impact on ecology, evolution, coevolution, community assemblages, and the evolution of niches.

SUMMARY POINTS

1. Continuous-trait game theory is a modeling tool whose use is rapidly growing owing to its unique ability to address real-world questions in evolutionary ecology that involve complex traits in a density- and frequency-dependent context.

2. The key innovation of game theory relative to optimization theory is examining the fitness $W(u, U)$ of a rare mutant, u, playing against the field, U. An evolutionarily stable strategy (ESS) is one that is its own best response; at an ESS an individual maximizes its fitness by playing the same strategy as the population, which makes an ESS resistant to invasion by rare alternative strategies.

3. Adaptive dynamics extends the static nature of game theory by exploring the dynamic processes that lead a population to evolve toward an ESS. Surprisingly, evolution can lead to fitness minima as well as ESSs being evolutionary repellors. Adaptive dynamics highlights the importance of convergence stability (being an evolutionary attractor).

4. We propose clarification of the convoluted terminology of game theory. We suggest defining an ESS as a strategy or coalition of strategies that is a fitness maximum (invasion-resistant) and convergent stable (evolutionarily attracting). Branching points are fitness minima yet still evolutionary attractors (convergent stable). Finally, evolutionary repellors are strategies that are not convergent stable regardless of whether they are maxima or minima.

5. The notion of an ESS extends easily to (*a*) coalitions of coexisting populations or species with distinct strategies, (*b*) nonequilibrium population dynamics, (*c*) stochastic environments (*d*) stage-structured populations (*e*) multiple traits, and (*f*) coevolution of multiple species.

6. Continuous-trait game theory has been applied to a wide variety of questions in evolutionary ecology, including evolution of phenology, germination, nutrient foraging in plants, predator-prey foraging, offspring size-number, dispersal, and coevolution.

FUTURE ISSUES

1. Continuous-trait game theory needs to rise to the challenge of its critics (Waxman & Gavrilets 2005) and produce strong predictions that can be tested. We believe the best way to do this is through the development of applied models rather than more theoretical development. This goal leads immediately to the next three items below.

2. The mathematical development of game theory is important but must stop reveling in small differences between theories and instead emphasize the underlying unity of game theory as a language for natural selection. This will make game theory more attractive and accessible to those simply interested in evolution and not game theory in particular. Similarity of new work to preexisting concepts should be highlighted. The proliferation of terminology is excessive and has been detrimental to the field.

3. Collaborations between mathematical modelers and field ecologists are needed to develop applications of continuous-trait game theory to biologically important questions. This requires models to be less heuristic and more amenable to empirical test.

4. Models need to make stronger predictions. Many existing models produce weak predictions. For example, a prediction that an intermediate germination fraction (that is, >0 and <1) is an ESS counts as a weak prediction. Stronger predictions would include predictions that the germination fraction will increase or decrease with increasing environmental noise, environmental autocorrelation, etc.

5. Although developing new and better applications remains the most important future direction, additional mathematical development is also needed on specific topics such as the evolution of multiple traits, evolution in a stochastic environment, tractable conditions for convergence stability in Lyapunov and multitrait/multispecies models, and bifurcation theory. Further exploration of unusual outcomes that occur only in atypical models and of evolution in cyclic or chaotic populations are probably not high priorities.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

Abrams PA. 2001. Adaptive dynamics: neither F nor G. *Evol. Ecol. Res.* 3:369–73

Abrams PA, Harada Y, Matsuda H. 1993a. On the relationship between quantitative genetics and ESS models. *Evolution* 47:982–85

Abrams PA, Matsuda H. 1997a. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. *Evol. Ecol.* 11:1–20

Abrams PA, Matsuda H. 1997b. Prey adaptation as a cause of predator-prey cycles. *Evolution* 51:1742–50

Abrams PA, Matsuda H, Harada Y. 1993b. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.* 7:465–87

Abramsky Z, Rosenzweig ML, Pinshow B. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. *Ecology* 72:329–40

Abramsky Z, Rosenzweig ML, Subach A. 1997. Gerbils under threat of owl predation: isoclines and isodars. *Oikos* 78:81–90

Apaloo J, Muir PW, Hearne JW. 2005. Multi-species evolutionary dynamics. *Evol. Ecol.* 19:55–77

Auslander D, Guckenheimer J, Oster G. 1978. Random evolutionarily stable strategies. *Theor. Popul. Biol.* 13:276–93

Bever JD. 1999. Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. *Ecol. Lett.* 2:52–61

Bowers RG, White A, Boots M, Geritz SAH, Kisdi E. 2003. Evolutionary branching/speciation: contrasting results from systems with explicit or emergent carrying capacities. *Evol. Ecol. Res.* 5:883–91

Brew JS. 1982. Niche shift and the minimization of competition. *Theor. Popul. Biol.* 22:367–81

Brown JS. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Soc.* 22:37–47

Brown JS. 1990a. Community organization under predator-prey coevolution. See Vincent et al. 1990, pp. 263–88

Brown JS. 1990b. Habitat selection as an evolutionary game. *Evolution* 44:732–46

Brown JS. 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evol. Ecol.* 6:360–82

Brown JS. 1998. Game theory and habitat selection. In *Game Theory and Animal Behavior*, ed. LA Dugatkin, HK Reeve, pp. 188–220. New York: Oxford Univ. Press

Brown JS. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.* 1:49–71

Brown JS, Pavlovic NB. 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evol. Ecol.* 6:360–82

Brown JS, Vincent TL. 1987a. Coevolution as an evolutionary game. *Evolution* 41:66–79

Brown JS, Vincent TL. 1987b. A theory for the evolutionary game. *Theor. Popul. Biol.* 31:140–66

Brown JS, Vincent TL. 1992. Organization of predator-prey communities as an evolutionary game. *Evolution* 46:1269–83

Bulmer M. 1983. Models for the evolution of protandry in insects. *Theor. Popul. Biol.* 23:314–22

Bulmer M. 1984. Delayed germination of seeds: Cohen's model revisited. *Theor. Popul. Biol.* 26:367–77

Bulmer M. 1994. *Theoretical Evolutionary Ecology*. Sunderland, MA: Sinauer

Caswell H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sunderland, MA: Sinauer

Christiansen FB. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.* 138:37–50

Cohen D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* 12:119–29

Cohen D, Levin SA. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. *Theor. Popul. Biol.* 39:63–99

Cohen Y. 2003. Distributed evolutionary games. *Evol. Ecol. Res.* 5:383–96

Cohen Y, Vincent TL, Brown JS. 1999. A G-function approach to fitness minima, fitness maxima, evolutionarily stable strategies and adaptive landscapes. *Evol. Ecol. Res.* 1:923–42

Cohen Y, Vincent TL, Brown JS. 2001. Does the G-function deserve an F? *Evol. Ecol. Res.* 3:375–77

Comins HN, Hamilton WD, May RM. 1980. Evolutionarily stable dispersal strategies. *J. Theor. Biol.* 82:205–30

Cressman R, Garay J. 2003. Stability in n-species coevolutionary systems. *Theor. Popul. Biol.* 64:519–33

Crow JF, Kimura M. 1970. *An Introduction to Population Genetics Theory*. New York: Harper & Row

Cushing JM, Costantino RF, Dennis B, Desharnis R, Henson SM. 2002. *Chaos in Ecology: Experimental Nonlinear Dynamics*. San Diego, CA: Academic

Day T, Taylor PD. 2003. Evolutionary dynamics and stability in discrete and continuous games. *Evol. Ecol. Res.* 5:605–13

de Mazancourt C, Dieckmann U. 2004. Trade-off geometries and frequency-dependent selection. *Am. Nat.* 164:765–78

De Mazancourt C, Loreau M, Dieckmann U. 2005. Understanding mutualism when there is adaptation to the partner. *J. Ecol.* 93:305–14

Dieckmann U, Doebeli M. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–57

Dieckmann U, Law R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* 34:569–612

Dieckmann U, Marrow P, Law R. 1995. Evolutionary cycling in predator-prey interactions: population dynamics and the red queen. *J. Theor. Biol.* 176:91–102

Diekmann O, Christiansen F, Law R. 1996. Evolutionary dynamics. Editorial. *J. Math. Biol.* 34:483

Diekmann O, Mylius SD, ten Donkelaar JR. 1999. Saumon a la Kaitala et Getz, sauce hollandaise. *Evol. Ecol. Res.* 1:261–75

Doebeli M, Dieckmann U. 2000. Evolutionary branching and sympatric speciation caused by diffent types of ecological interactions. *Am. Nat.* 156:S77–101

Doebeli M, Dieckmann U. 2003. Speciation along environmental gradients. *Nature* 421:259–64

Doebeli M, Hauart C, Killingback T. 2004. The evolutionary origin of cooperators and defectors. *Science* 306:859–62

Doebeli M, Ruxton GD. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution* 51:1730–41

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

Ellner S. 1985b. ESS Germination strategies in randomly varying environments. II Reciprocal yield-law models. *Theor. Popul. Biol.* 28:80–116

Ellner S, Hairston NG Jr. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *Am. Nat.* 143:403–17

Eshel I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.* 103:99–111

Ezoe H. 1998. Optimal dispersal range and seed size in a stable environment. *J. Theor. Biol.* 190:287–93

Ezoe H, Iwasa Y. 1997. Evolution of condition-dependent dispersals: a genetic algorithm search for the ESS reaction norm. *Res. Popul. Ecol.* 39:127–37

Falster DS, Westoby M. 2003. Plant height and evolutionary games. *Trends Ecol. Evol.* 18:337–43

Ferrière R. 2000. Adaptive responses to environmental threats: evolutionary suicide, insurance and rescue. *Options 2000*, pp. 12–16. Laxenburg, Austria: Int. Inst. Appl. Syst. Anal.

Ferrière R, Gatto M. 1995. Lyapunov exponents and the mathematics of invasion in oscillatory or chaotic populations. *Theor. Popul. Biol.* 48:126–71

Fisher RA. 1930. *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press

Flaxman SM, Reeve HK. 2006. Putting competition strategies into ideal free distribution models: habitat selection as a tug of war. *J. Theor. Biol.* 243:587–93

Frank SA. 1997. The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis. *Evolution* 51:1712–29

Fretwell SD. 1972. *Populations in a Seasonal Environment*. Princeton, NJ: Princeton Univ. Press

Fretwell SD, Lucas HLJ. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* 19:16–36

Fudenberg D, Harris C. 1992. Evolutionary dynamics with aggregate shocks. *J. Econ. Theory* 57:420–41

Geritz SAH. 1995. Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density. *Am. Nat.* 146:685–707

Geritz SAH. 1998. Co-evolution of seed size and seed predation. *Evol. Ecol.* 12:891–911

Geritz SAH, Gyllenberg M, Jacobs FJA, Parvinen K. 2002. Invasion dynamics and attractor inheritance. *Math. Biol.* 44:548–60

Geritz SAH, Gyllenberg M, Yan P. 2006. Plant growth and the optimal sharing of photsynthetic products with a mycorrhizal symbiont. *Evol. Ecol. Res.* 8:577–90

Geritz SAH, Kisdi E. 2000. Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proc. R. Soc. London Ser. B* 267:1671–78

Geritz SAH, Kisdi E, Meszena G, Metz JAJ. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* 12:35–57

Geritz SAH, Metz JAJ, Kisdi E, Meszena G. 1997. Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.* 78:2024–27

Geritz SAH, Van Der Meijden E, Metz JAJ. 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theor. Popul. Biol.* 55:324–43

Gintis H. 2000. *Game Theory Evolving: A Problem-Centered Introduction to Modeling Strategic Interaction*. Princeton, NJ: Princeton Univ. Press

Goodman D. 1984. Risk spreading as an adaptive strategy in iteroparous life histories. *Theor. Popul. Biol.* 25:1–20

Gyllenberg M, Metz JAJ. 2001. On fitness in structured metapopulations. *J. Math. Biol.* 43:545–60

Gyllenberg M, Parvinen K, Dieckmann U. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.* 45:79–105

Hamilton WD. 1967. Extraordinary sex ratios. *Science* 156:477–88

Hofbauer J. 1996. Evolutionary dynamics for bimatrix games: a Hamiltonian system? *J. Math. Biol.* 34:675–88

Holt RD, McPeek MA. 1996. Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* 148:709–18

Iwasa Y, Haccou P. 1994. ESS emergence pattern of male butterflies in stochastic environments. *Evol. Ecol.* 8:503–23

Iwasa Y, Levin SA. 1995. The timing of life-history events. *J. Theor. Biol.* 172:33–42

Iwasa Y, Odendaal FJ, Murphy DD, Ehrlich PR, Launer AE. 1983. Emergence patterns in male butterflies: a hypothesis and a test. *Theor. Popul. Biol.* 23:363–79

Kaitala A, Kaitala V, Lundberg P. 1993. A theory of partial migration. *Am. Nat.* 142:59–81

Kisdi E. 2002. Dispersal: risk spreading vs local adaptation. *Am. Nat.* 159:579–96

Kisdi E. 2004. Conditional dispersal under kin competition: extension of the Hamilton-May model to brood size-dependent dispersal. *Theor. Popul. Biol.* 66:369–80

Kisdi E. 2006. Trade-off geometries and the adaptive dynamics of two coevolving species. *Evol. Ecol. Res.* 8:959–73

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

Kokko H. 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* 68:940–50

Kokko H, Johnstone RA. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. *Proc. R. Soc. London Ser. B* 266:571–78

Kondrashov AS. 1986. Sympatric speciation: when is it possible. *Biol. J. Linn. Soc.* 27:201–23

Kondrashov AS, Kondrashov FA. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* 400:351–54

Lande R. 1979. Quantitative genetic analysis of multivariate evolution applied to brain-body size allometry. *Evolution* 33:402–16

Lavorel S, ONeill RV, Gardner RH. 1994. Spatiotemporal dispersal strategies and annual plant-species coexistence in a structured landscape. *Oikos* 71:75–88

Lawlor LR, Maynard-Smith J. 1976. The coevolution and stability of competing species. *Am. Nat.* 110:79–99

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

Leimar O. 2007. Multidimensional convergence stability and the canonical adaptive dynamics. In *Elements of Adaptive Dynamics*, ed. U Dieckmann, JAJ Metz. Cambridge, UK: Cambridge Univ. Press. In press

Lemel JY, Belichon S, Clobert J, Hochberg ME. 1997. The evolution of dispersal in a two-patch system: some consequences of diferences between migrants and residents. *Evol. Ecol.* 11:613–29

Lessard S. 1990. Evolutionary stability: One concept, several meanings. *Theor. Popul. Biol.* 37:159–70

Levene H. 1953. Genetic equilibrium when more than one ecological niche is available. *Am. Nat.* 87:331–32

Levin SA, Cohen D, Hastings A. 1984. Dispersal strategies in patchy environments. *Theor. Popul. Biol.* 26:165–91

Levin SA, Muller-Landau HC. 2000. The evolution of dispersal and seed size in plant communities. *Evol. Ecol. Res.* 2:409–35

Levins R. 1968. *Evolution in Changing Environments*. Princeton, NJ: Princeton Univ. Press. ix+120 pp.

Luce RD, Raiffa H. 1957. *Games and Decisions: Introduction and Critical Survey*. New York: Wiley

Ludwig D, Levin SA. 1991. Evolutionary stability of plant communities and the maintenance of multiple dispersal types. *Theor. Popul. Biol.* 40:285–307

Lytle DA. 2001. Disturbance regimes and life-history evolution. *Am. Nat.* 157:525–36

MacArthur RH. 1967. The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.* 101:377–85

Matessi C, Di Pasquale C. 1996. Long-term evolution of multilocus traits. *J. Math. Biol.* 34:613–53

Matessi C, Jayakar SD. 1976. Conditions for the evolution of altruism under Darwinian selection. *Theor. Popul. Biol.* 9:360–87

Mathias A, Kisdi E. 2002. Adaptive diversification of germination strategies. *Proc. R. Soc. London Ser. B* 269:151–55

Mathias A, Kisdi E, Olivieri I. 2001. Divergent evolution of dispersal in a heterogeneous landscape. *Evolution* 55:246–59

Maynard-Smith J. 1981. Will a sexual population evolve to an ESS? *Am. Nat.* 117:1015–18

Maynard-Smith J. 1982. *Evolution and the Theory of Games*. Cambridge, UK: Cambridge Univ. Press. 224 pp.

Maynard Smith J. 1966. Sympatric speciation. *Am. Nat.* 100:637–50

Maynard Smith J, Price GR. 1973. The logic of animal conflict. *Nature* 246:15–18

McGill BJ. 2005. A mechanistic model of a mutualism and its ecologicaland evolutionary dynamics. *Ecol. Model.* 187:413–25

Metz JAJ, Geritz SAH, Meszena G, Jacobs FJA, van Heerwaarden J. 1996. Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems*, ed. SJ van Strien, SM Verduyn-Lunel, pp. 183–231. Amsterdam: KNAW Verhandelingen

Metz JAJ, Nisbet RM, Geritz SAH. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.* 7:198–202

Mitchell WA. 2000. Limits to species richness in a continuum of habitat heterogeni-ety: an ESS approach. *Evol. Ecol. Res.* 2:293–316

Motro U. 1982. Optimal rates of dispersal I. Haploid populations. *Theor. Popul. Biol.* 21:394–411

Motro U. 1983. Optimal rates of dispersal. III. Parent-offspring conflict. *Theor. Popul. Biol.* 23:159–68

Nash J. 1950. Equilibrium points in n-person games. *Proc. Natl. Acad Sci. USA* 36:48–49

Parker GA, Courntey P. 1983. Seasonal incidence: adaptive variation in the timing of life history stages. *J. Theor. Biol.* 105:147–55

Parvinen K. 1999. Evolution of migration in a metapopultaion. *Bull. Math. Biol.* 61:531–50

Rand DA, Wilson HB, McGlade JM. 1994. Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics. *Philos. Trans. R. Soc. London Ser. B* 343:261–83

Rees M, Westoby M. 1997. Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos* 78:116–26

Reeve HK, Dugatkin LA, eds. 1998. *Game Theory and Animal Behavior*. New York: Oxford Univ. Press

Roff D. 2002. *Life History Evolution*. Sunderland, MA: Sinauer

Ronce O, Gandon S, Rousset F. 2000. Kin selection and natal dispersal in an age-structured population. *Theor. Popul. Biol.* 58:143–59

Rosenzweig ML. 1978. Competitive speciation. *Biol. J. Linn. Soc.* 10:275–89

Rosenzweig ML. 1981. A theory of habitat selection. *Ecology* 62:327–35

Rosenzweig ML. 1987. Habitat selection as a source of biological diversity. *Evol. Ecol.* 1:315–30

Roughgarden J. 1976. Resource partitioning among competing species—a coevolu-tionary approach. *Theor. Popul. Biol.* 9:338–424

Roughgarden J. 1979. *Theory of Population Genetics and Evolutionary Ecology: An Intro-duction*. New York: Macmillan. 612 pp.

Roughgarden J. 1983. The theory of coevolution. In *Coevolution*, ed. DJ Futuyma, M Slatkin, pp. 33–64. Sunderland, MA: Sinauer

Schmidt KA, Earnhardt JM, Brown JS, Holt RD. 2000. Habitat selection under tem-poral heterogeneity: exorcising the ghost of competition past. *Ecology* 81:2622–30

Seger J, Brockmann HJ. 1987. What is bet-hedging? In *Oxford Surveys in Evolutionary Biology*, ed. PH Harvey, L Partridge, pp. 183–211. Oxford: Oxford Univ. Press

Smith CC, Fretwell SD. 1974. The optimal balance between size and number of offspring. *Am. Nat.* 108:499–506

Stephens PA, Russell AF, Young AJ, Sutherland WJ, Clutton-Brock TH. 2005. Dis-persal, eviction and conflict in meerkats (Suricata suricatta): an evolutionarily stable strategy model. *Am. Nat.* 165:120–35

Taylor PD. 1989. Local stability in seed provisioning model. *J. Theor. Biol.* 136:1–12

Taylor PD, Frank SA. 1996. How to make a kin selection model. *J. Theor. Biol.* 180:27–37

Thoday JM, Gibson JB. 1962. Isolation by disruptive selection. *Nature* 193:1164–66

Tregenza T, Butlin RK. 1999. Speciation without isolation. *Nature* 400:311–12

Tuljapurkar SD. 1990. *Population Dynamics in Variable Environments*. New York: Springer-Verlag

Tuljapurkar SD. 1997. Stochastic matrix models. In *Structured-Population Models in Marine, Terrestrial and Freshwater Systems*, ed. SD Tuljapurkar, H Caswell, pp. 59–87. New York: Chapman & Hall

Tuljapurkar SD, Istock C. 1993. Environmental uncertainty and variable diapuse. *Theor. Popul. Biol.* 43:251–80

Tuljapurkar SD, Orzack SH. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor. Popul. Biol.* 18:314–42

Venable DL, Brown JS. 1988. The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* 131:360–84

Venable DL, Brown JS. 1993. The seed population-dynamic functions of seed dispersal. In *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects. Vegetatio* 107/108, ed. TH Fleming, A Estrada, pp. 31–55. Dordrecht: Kluwer

Vincent TL. 1990. Strategy dynamics and the ESS. See Vincent et al. 1990, pp. 236–62

Vincent TL, Brown JS. 1984. Stability in an evolutionary game. *Theor. Popul. Biol.* 26:408–27

Vincent TL, Brown JS. 1987. Evolution under nonequilibrium dynamics. *Math. Model.* 8:766–71

Vincent TL, Brown JS. 1988. The evolution of ESS theory. *Annu. Rev. Ecol. Syst.* 19:423–43

Vincent TL, Brown JS. 2001. Evolutionarily stable strategies in multistage biological systems. *Selection* 2:85–102

Vincent TL, Brown JS. 2005. *Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics*. Cambridge, UK: Cambridge Univ. Press. 400 pp.

Vincent TL, Cohen Y, Brown JS. 1993. Evolution via strategy dynamics. *Theor. Popul. Biol.* 44:149–76

Vincent TL, Cressman R. 2000. An ESS maximum principle for matrix games. *Theor. Popul. Biol.* 58:173–86

Vincent TL, Mees AI, Jennings LS, eds. 1990. *Dynamics of Complex Interconnected Biological Systems*. Boston: Birkhauser

Vincent TL, Van MV, Goh BS. 1996. Ecological stability, evolutionary stability and the ESS maximum principle. *Evol. Ecol.* 10:567–91

Vincent TLS, Scheel D, Brown JS, Vincent TL. 1996. Trade-offs and coexistence in consumer-resource models: it all depends what and where you eat. Am. Nat. 148:1038–58

von Neumann J, Morgenstern O. 1944. *Theory of Games and Economic Behaviour*. Princeton, NJ: Princeton University Press

Waxman D, Gavrilets S. 2005. 20 questions on adaptive dynamics. *J. Evol. Biol.* 18:1139–54

Wiklund C, Wickman PO, Nylin S. 1992. A sex difference in the propensity to enter direct/diapuse development—a result of selection for protandry. *Evolution* 46:519–28

Winkler E, Fischer M. 1999. Two fitness measures for clonal plants and the impor-
tance of spatial aspects. *Plant Ecol.* 141:191–99

Wright S. 1930. Evolution in Mendellian populations. *Genetics* 16:97–159

Yoshida T, Jones LE, Ellner SP, Fussmann GF, Hairston NGJ. 2003. Rapid evolution
drives ecological dynamics in a predator-prey system. *Nature* 424:303–6

Yoshimura J, Clark CW. 1991. Individual adaptation in stochastic environments. *Evol.
Ecol.* 5:173–92