

Adaptive Dynamics

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Key Points

- Adaptive Dynamics is a method for modelling the eco-evolutionary dynamics of quantitative traits
- By assuming mutations are rare and have small effects, it is possible to determine the invasion fitness of a rare mutant
- A trait will evolve in the direction of the selection gradient until the gradient reaches zero, which may represent an evolutionary endpoint or a branching point leading to diversification
- The method can be readily extended to consider coevolution and non-equilibrium dynamics

Glossary

Branching point A singular strategy that is convergence stable but not evolutionarily stable, resulting in disruptive selection and the emergence of two coexisting phenotypes from a previously monomorphic population.

Continuously stable strategy A singular strategy that is both convergence and evolutionarily stable, representing an endpoint to the evolutionary process.

Convergence stability A singular strategy is convergence stable if evolutionary trajectories tend towards it.

Eco-evolutionary feedback The impact of ecological (population) dynamics on evolutionary (trait) dynamics, and vice versa.

Evolutionary stability A singular strategy is evolutionarily stable if it is uninvadable by similar phenotypes.

Invasion fitness The growth rate of a rare mutant in an established resident population.

Selection gradient The strength and direction of selection, given by the derivative of invasion fitness with respect to the mutant phenotype, evaluated at the resident trait value.

Singular strategy A point in phenotype space where the selection gradient vanishes.

Abstract

Adaptive Dynamics is a widely used approach to model the evolution of quantitative traits. Its roots lie in quantitative genetics and evolutionary game theory, but its strengths lie in its ability to simultaneously capture ecological and evolutionary dynamics while maintaining analytic tractability. Today, Adaptive Dynamics is applied to a broad range of topics across evolutionary biology, from evolutionary epidemiology to sexual selection to altruism. Here, we discuss the foundations of Adaptive Dynamics and illustrate how the framework can be applied to understand eco-evolutionary dynamics.

Introduction

Mathematics has a rich and diverse history in evolutionary biology. From the inception of mathematical population genetics during the early 20th century by Fisher (1922) and Haldane (1927), to Wright's "adaptive landscape" (Wright, 1932), Hamilton's concept of inclusive fitness (Hamilton, 1964) and the development of evolutionary game theory by Maynard Smith (1982), mathematical models have played a key role in shaping our understanding of biological evolution.

However, many approaches, while providing fundamental insights into evolution, typically downplay or neglect the role of feedbacks between ecological and evolutionary processes. To illustrate why these feedbacks matter, consider a population that is initially susceptible to an infectious disease except for a small number of hosts with an allele (variant of a gene) that prevents infection but also incurs a fitness cost (e.g., lower fecundity or higher mortality). If the expected cost of disease—taking into account both the risk of infection and severity of disease—is higher than the cost of resistance, then the resistance allele will increase in frequency. However, as the allele becomes more common, a smaller proportion of the host population can be infected and so disease prevalence, and hence the risk of infection, begins to fall. Crucially, the expected cost of disease declines as well since all hosts are less likely to encounter the pathogen, reducing the strength of selection for resistance. Eventually, the frequency of the resistance allele reaches a point where its intrinsic fitness cost is perfectly balanced by the expected cost of infection, leading to stable polymorphism of susceptible and resistant hosts and an endemic infectious disease. Hence the fitness landscape is dynamic and changes depending on the ecological context. If the changing ecological (or in this case, epidemiological) environment is not accounted for, then the fitness landscape is static and so the resistance allele sweeps to fixation and eliminates the pathogen. Clearly, feedbacks between ecology and evolution can significantly affect how processes at both scales unfold (Ashby et al., 2019).

Adaptive Dynamics, also known as evolutionary invasion analysis, emerged during the latter stages of the 20th century as a method for modelling phenotypic evolution (i.e., the evolution of quantitative traits) by fully capturing feedbacks between ecological and evolutionary processes (Dieckmann and Law, 1996; Geritz et al., 1998). This marks an important difference with classical population genetics and quantitative genetics, where the underlying ecology may be neglected and fitness may be defined arbitrarily or uncoupled from specific ecological processes. Adaptive Dynamics is able to capture these feedbacks by focusing on long-term rather than short-term outcomes, which greatly reduces model complexity by ignoring transient dynamics (see *Key assumptions*). By focusing primarily on potential endpoints of an evolutionary process, it draws on the concept of an *Evolutionarily Stable Strategy* or *ESS* from evolutionary game theory (Maynard Smith, 1982), but also considers a dynamical process of evolution to determine if a potential endpoint can be reached through gradual invasion and replacement of phenotypes (Dieckmann and Law, 1996; Geritz et al., 1998). Moreover, what may at first appear to be an evolutionary endpoint may in fact be the start of another evolutionary process due to the changing fitness landscape.

The Adaptive Dynamics framework has been applied to a wide range of topics across evolutionary biology, including: host and pathogen evolution (Boots and Haraguchi, 1999; Best et al., 2008, 2010; Boldin et al., 2009), symbiosis (Ashby and King, 2017; Smith and Ashby, 2023), resource competition and niche width (Ackermann and Doebeli, 2004), altruism (van Baalen and Rand, 1998), dispersal (Levin and Muller-Landau, 2000), speciation (Dieckmann and Doebeli, 1999), coevolution (Ashby and Boots, 2015; Best et al., 2010; Kisdí, 2006), evolutionary suicide (Gyllenberg and Parvinen, 2001) and sexual selection (Ashby and Boots, 2015; van Doorn et al., 2004). The framework's broad applicability arises from the fact that it makes relatively few (albeit crucial) assumptions about how often mutations occur and the size of their effects, so that in principle the evolution of any trait could be modelled using Adaptive Dynamics.

Key Assumptions

Adaptive Dynamics makes three key assumptions about the nature of mutations. First, it assumes that mutations are sufficiently rare that the population reaches a *dynamic attractor* (often, but not necessarily, an equilibrium) before a new mutant arises. This leads to a separation of ecological (population dynamics) and evolutionary (phenotypic dynamics) timescales, which greatly simplifies the analysis. Second, Adaptive Dynamics assumes that mutants themselves are initially rare relative to the resident phenotype(s) in the population. This means that the mutant initially has a negligible effect on the rest of the population, and so one can consider its fate (to increase in frequency or be purged) in terms of its growth rate when rare (*invasion fitness*) without having to also consider the dynamics of the resident population. Again, this greatly simplifies the analysis as one need only consider the fate of a single phenotype (i.e., the mutant) in a given environment, rather than the fates of multiple phenotypes (i.e., the mutant and resident(s)) simultaneously.

The third and final key assumption is that the mutant is phenotypically similar to a resident phenotype. This means that phenotypes are treated as quantitative traits controlled by many genetic loci with small additive effects (i.e., no epistasis). Hence, mutations in phenotype space are local, which means that the direction of evolution is determined by the selection gradient, leading to a gradual process of invasion and replacement rather than sudden drastic changes in phenotypes. Together, these assumptions imply that Adaptive Dynamics is a special case of quantitative genetics, with no standing genetic variation as selection always dominates mutation because the latter is "rare". This means that rather than the population consisting of a distribution of phenotypes with a given mean and positive variance, the distribution of phenotypes is concentrated entirely at the mean with no variance (at least initially).

The Canonical Equation of Adaptive Dynamics

One can describe phenotypic evolution in a large, monomorphic, asexual population with rare mutations using the “canonical equation of Adaptive Dynamics” (Dieckmann and Law, 1996):

$$\frac{dx}{dt} = \frac{1}{2} \mu \sigma^2 N^*(x) \left. \frac{\partial s(x_m, x)}{\partial x_m} \right|_{x_m=x} \quad (1)$$

where x is the value of the trait under selection, μ is the per capita mutation rate, σ^2 describes the variance of mutation effects, $N^*(x)$ is the population size (or density) at equilibrium, and $s(x_m, x)$ is the *invasion fitness* or per capita growth rate of a rare mutant with trait value x_m in a resident population with trait value x . Note that the canonical equation assumes that phenotypes are continuous and is therefore a limit of the more realistic assumption that mutations have small but discrete effects.

The right hand side of the equation is essentially the product of two factors that are necessary for evolution by natural selection: mutation supply and a *selection gradient*. The first four elements of the equation ($\frac{1}{2} \mu \sigma^2 N^*(x)$) determine the mutation supply upon which selection can act. The product of μ and $N^*(x)$ gives the total rate at which mutations arise in the population, and σ^2 gives the distribution of mutation effect sizes, with larger variances corresponding to faster rates of adaptation. The factor of $\frac{1}{2}$ represents unbiased mutation because on average half of mutations will have effects in the opposite direction to the selection gradient, which is given by the final factor in the equation, $\left. \frac{\partial s(x_m, x)}{\partial x_m} \right|_{x_m=x}$. The selection gradient is equal to the partial derivative of invasion fitness with respect to the mutant’s phenotype, which is then evaluated at the resident’s phenotype. The selection gradient gives the strength and direction of selection in the monomorphic resident population prior to a new mutant arising. Evolution proceeds through a gradual process of invasion and replacement of phenotypes until a singular strategy, x^* , is reached at

$$\left. \frac{\partial s(x_m, x)}{\partial x_m} \right|_{x_m=x^*} = 0 \quad (2)$$

A singular strategy represents a potential endpoint of evolution. Assuming the mutation supply is always positive and the population is not extinct (although it is possible for populations to be driven extinct through a process known as evolutionary suicide (Gyllenberg and Parvinen, 2001)), a singular strategy can only be reached when the selection gradient equals zero.

Evolutionary Invasion Analysis

Ecological Dynamics

To illustrate the process of constructing and carrying out evolutionary invasion analysis using the Adaptive Dynamics framework, consider a relatively simple large population that is well-mixed, asexual, and monomorphic, and whose changes population density N according to logistic growth:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K(x)} \right) \quad (3)$$

where $r > 0$ is the intrinsic growth rate of the population and $K(x) > 0$ is its carrying capacity, which we assume depends on its phenotype, x . For example, x could represent beak size in birds, which affects the types of seeds that can be consumed. If some types of seeds are more abundant in the environment, then the carrying capacity can be expressed as a function of the types of seeds that birds can eat. Alternatively, x could represent body size, with the environment potentially able to support more smaller individuals. More generally, x could represent any trait that affects survival or reproductive success including pH or temperature preference, breeding season or nesting location, susceptibility to infection or predation, and secondary sex ornaments.

Before considering the fate of a rare mutant, we must ensure that the resident population reaches a *dynamic attractor* in the form of an equilibrium, or possibly a limit cycle (Best and Ashby, 2023). Using linear stability analysis, it is straightforward to show that the population in this case will tend towards its carrying capacity in the long-term and so we may proceed (in mathematical terms, the carrying capacity is said to be locally asymptotically stable, i.e., $N(t) \rightarrow N^*(x) = K(x)$ as $t \rightarrow \infty$).

Invasion Fitness, Selection Gradient, and Singular Strategies

Suppose a rare mutant arises in this population with phenotype $x_m \approx x$ and population density N_m . We will assume that the strength of competition between resident and mutant phenotypes is given by $a(x_m, x)$ and is maximised at 1 when $x_m = x$, so that organisms with more similar phenotypes compete more strongly than organisms that are dissimilar. The invasion dynamics of this mutant are then given by

$$s(x_m, x) = \frac{1}{N_m} \frac{dN_m}{dt} \approx r \left(1 - \frac{a(x_m, x) N^*(x)}{K(x_m)} \right) = r \left(1 - \frac{a(x_m, x) K(x)}{K(x_m)} \right) \quad (4)$$

where $s(x_m, x)$ is the invasion fitness of the mutant. Intuitively, when the mutant has positive invasion fitness it will increase in frequency in the population (i.e., it will invade), and when the mutant has negative invasion fitness it will be driven extinct. From the expression above, we see that a mutant can invade when

$$\frac{K(x_m)}{a(x_m, x)} > K(x) \quad (5)$$

This means that the mutant can invade provided any increase (or decrease) in the strength of competition that it experiences is offset by a greater increase (or lesser reduction) in its carrying capacity. Note that the fate of a mutant depends on the resident trait, x , as the resident phenotype determines the environment in which the mutant arises. In this relatively simple case where the invasion dynamics only depend on a single equation, invasion fitness is equal to the per capita growth rate of the rare mutant. However, if the invasion dynamics require multiple equations (e.g., if the population is structured by age or sex), then invasion fitness is given by the sign of the leading eigenvalue of the Jacobian matrix of the mutant dynamics. In practice, it is often easier to find the largest eigenvalue of the corresponding next-generation matrix (Hurford et al., 2010), which then serves as a proxy to invasion fitness.

Invasion fitness determines whether a mutant will spread through the population or be purged. Usually, one is concerned not just with the fate of a single mutant, but with the evolutionary trajectory of a population, given by the canonical equation of Adaptive Dynamics (Eq. (1)). To determine the direction of evolution, one must first find the selection gradient, which for the model above is

$$\left. \frac{\partial s}{\partial x_m} \right|_{x_m=x} = r \left(\frac{K'(x)}{K(x)} - \left. \frac{\partial a}{\partial x_m} \right|_{x_m=x} \right) \quad (6)$$

$$= \frac{rK'(x)}{K(x)} \quad (7)$$

since the gradient of $a(x, x)$ is zero given its assumed form. A singular strategy must satisfy $K'(x^*) = 0$, which implies that the population will initially evolve to maximise the carrying capacity.

Evolutionary and Convergence Stability

A singular strategy may represent an endpoint of the evolutionary process, but not necessarily. To determine what happens after the population reaches a singular strategy, one must consider the second-order derivatives of invasion fitness, which determine whether a singular strategy is *evolutionarily stable* and *convergence stable*. A singular strategy is said to be evolutionarily stable if it is uninvadable by all nearby mutants. In other words, it must be a *local fitness maximum*, which requires

$$E = \left. \frac{\partial^2 s}{\partial x_m^2} \right|_{x_m=x=x^*} < 0 \quad (8)$$

Evolutionary stability is analogous to the classical concept of an *Evolutionarily Stable Strategy* or *ESS* in evolutionary game theory. Convergence stability, on the other hand, is analogous to asymptotic stability in dynamical systems, requiring all mutants closer to the singular strategy to be fitter than the current resident population. The sign of the selection gradient must change from positive for $x < x^*$ to negative for $x > x^*$, which requires

$$C = E + \left. \frac{\partial^2 s}{\partial x_m \partial x} \right|_{x_m=x=x^*} = E + M < 0 \quad (9)$$

where the quantity M tells us if the singular strategy can be invaded by nearby mutants and vice versa (*mutual invasibility*). Equivalently, (by noting that the second-order directional derivative along $x_m = x$ is 0), convergence stability requires

$$\left. \frac{\partial^2 s}{\partial x_m^2} \right|_{x_m=x=x^*} < \left. \frac{\partial^2 s}{\partial x^2} \right|_{x_m=x=x^*} \quad (10)$$

Clearly, a singular strategy can be evolutionarily stable without being convergence stable, and vice versa, giving four possible classifications for a singular strategy. When a singular strategy is both evolutionarily stable ($E < 0$) and convergence stable ($C < 0$), the population evolves to a local fitness peak, which is uninvadable. This is known as a *Continuously Stable Strategy* or *CSS*, which represents an endpoint to the evolutionary process. In contrast, when a singular strategy is neither evolutionarily stable ($E > 0$) nor convergence stable ($C > 0$), the population evolves away from a local fitness minimum, which is an evolutionary *repeller*. When a singular strategy is evolutionarily stable ($E < 0$) but not convergence stable ($C > 0$), it is a local fitness peak that cannot be reached through gradual mutation and replacement of phenotypes. This is known as a *Garden of Eden*, in reference to the biblical paradise, as “Eden” is unobtainable. Finally, a singular strategy that is convergence stable ($C < 0$) but not evolutionarily stable ($E > 0$) is known as an evolutionary *branching point*. In this scenario, the population evolves towards a singular strategy but then experiences disruptive selection, leading to the emergence of a dimorphic population with two phenotypes, one on either side of the singular strategy. At this point, one must consider the dynamics of a system with two resident phenotypes. Note that mutual

invasibility ($M < 0$) is required for evolutionary branching to occur, but when only one trait is under selection, convergence stability and evolutionary instability together guarantee mutual invasibility. The same is not true when multiple traits are under selection (see *Coevolution* below).

A branching point may seem somewhat confusing at first. How can the population evolve to a singular strategy that is a fitness minimum? The apparent paradox is resolved by recognising that the singular strategy appears as a fitness peak from afar, but the topography of the fitness landscape changes as the population travels through phenotype space. The fitness landscape is not fixed but changes as the current resident population (which determines the environment that an invading mutant experiences) changes. This is known as an *eco-evolutionary feedback*, because the ecological (population) dynamics determine the environment in which a mutant arises (and hence the evolutionary dynamics), and the evolutionary (trait) dynamics determine which phenotypes dictate the ecological environment.

Returning to the example above, suppose $a(x_m, x) = \exp\left(-\frac{(x_m - x)^2}{2\sigma_a^2}\right)$ and $K(x) = K_0 \exp\left(-\frac{x^2}{2\sigma_K^2}\right)$ for some $\sigma_a, \sigma_K > 0$, which determine how quickly these functions decay to zero, and maximum carrying capacity $K_0 > 0$. The maximum carrying capacity is attained when $x^* = 0$, which is a singular strategy for the system. It can be shown that the singular strategy is always convergence stable, but is only evolutionarily stable when $\sigma_K < \sigma_a$. The population therefore evolves to a CSS and stays there when $\sigma_K < \sigma_a$ (i.e., mutants experience a sharper reduction in their carrying capacity than in the strength of competition), whereas the population undergoes evolutionary branching when $\sigma_K > \sigma_a$ (i.e., mutants experience a sharper reduction in their strength of competition than in their carrying capacity) (Fig. 1).

Often it is informative to graphically represent invasion fitness on a *Pairwise Invasion Plot* or *PIP*, which gives a more intuitive understanding of evolutionary and convergence stability (Fig. 2). PIPs also provide a geometric interpretation of the conditions for evolutionary and convergence stability. If it is possible to draw a vertical line through a singular strategy with both line segments immediately either side of the singular strategy falling in regions where the mutant has negative invasion fitness, then the singular strategy is evolutionarily stable. Similarly, if the mutant has positive invasion fitness immediately above the line $x_m = x$ to the left of the singular strategy, and immediately below the line $x_m = x$ to the right of the singular strategy, then it is convergence stable.

Extensions

We have now introduced the standard method for exploring evolutionary dynamics of a single trait under the assumptions of Adaptive Dynamics. This framework allows us to tackle a whole range of evolutionary questions. However, there are some scenarios where a little further work or assumptions are needed. Here we cover a few key extensions.

Coevolution

The complex reality of the natural world means that in most ecological systems there are multiple interacting organisms, all experiencing selection. What's more, the evolutionary trajectory of one species is likely to affect selection on the other. For example, in a host-parasite interaction, if a host evolves better defences we may well expect increased selection on the parasite to overcome those defences. We therefore would like to be able to model the simultaneous evolution—or coevolution—of multiple species. Similarly, one may wish to model the simultaneous evolution of multiple independent traits within a single species.

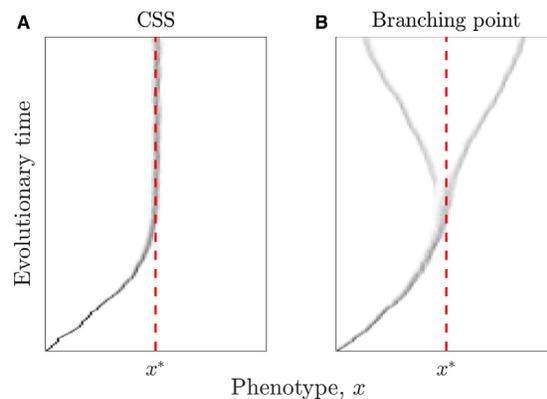


Fig. 1 Simulations of the resource competition model showing qualitatively different long-term evolutionary outcomes depending on how strongly changes in phenotype affect the strength of competition (σ_a) relative to effects of phenotype on the carrying capacity (σ_K). (A) When mutants experience a sharper reduction in their carrying capacity than in the strength of competition ($\sigma_K < \sigma_a$), the population evolves to a CSS. (B) When mutants experience a sharper reduction in their strength of competition than in their carrying capacity ($\sigma_K > \sigma_a$), the population experiences disruptive selection, leading to evolutionary branching into two distinct phenotypes.

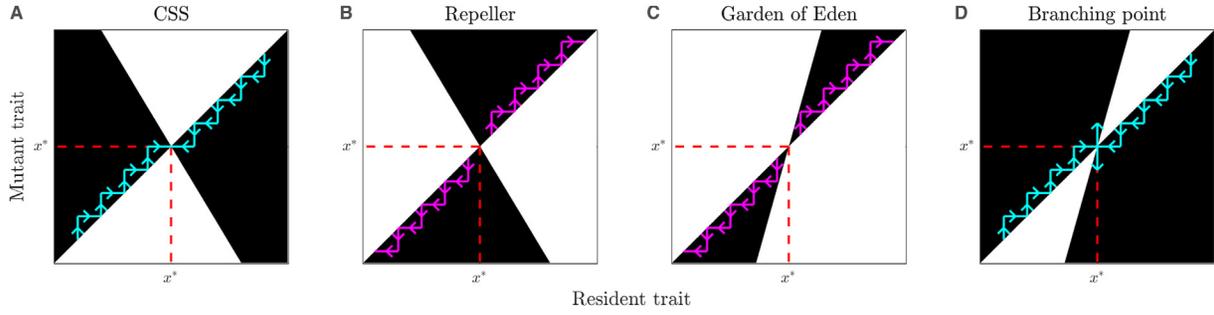


Fig. 2 Pairwise Invasion Plots (PIPs) with the four possible types of singular strategies, x^* : (A) a continuously stable strategy (CSS), that is both convergence stable ($C < 0$) and evolutionary stable ($E < 0$); (B) a repeller, that is neither convergence stable ($C > 0$) nor evolutionary stable ($E > 0$); (C) a Garden of Eden, that is evolutionarily stable ($E < 0$) but is not convergence stable ($C > 0$); and (D) a branching point, that is convergence stable ($C < 0$) but not evolutionarily stable ($E > 0$). Black and white regions indicate positive and negative invasion fitness, respectively. Lines with arrows indicate example evolutionary trajectories.

Fortunately, the starting point for a multi-trait model is the same as for a single-trait model. We first need to write down equations for the population dynamics of monomorphic resident phenotypes, and from these derive mutant invasion fitnesses for all traits that are under selection. As an example, consider a simple predator-prey system where the prey (N) can evolve lower susceptibility to predation, while the predator (P) can evolve to be more effective at catching prey. In the absence of any trade-offs, we would intuitively expect prey to minimise susceptibility to predation and predators will evolve maximum effectiveness at catching prey. We assume that both species experience trade-offs, such that lower susceptibility to predation comes at a cost of lower reproduction among prey and higher effectiveness at catching prey may come at a cost of higher mortality for predators. In both cases, such trade-offs may emerge due to the allocation of limited resources, for example to muscle growth for speed, or to secondary sex ornaments for attracting mates.

The resident population dynamics for this system are given by

$$\frac{dN}{dt} = a(\sigma)N - qN^2 - bN - \sigma\rho NP \quad (11)$$

$$\frac{dP}{dt} = c\sigma\rho NP - d(\rho)P, \quad (12)$$

where a is the prey growth (reproduction) rate, q represents the strength of competition for resources among prey, b is the prey mortality rate, c is the conversion efficiency for the predator (how well the predator converts prey biomass to reproduction) and d is the predator's death rate. The two traits under selection are σ —the prey's susceptibility to predation—and ρ —the predation effectiveness of predators. We can then derive the invasion fitness for mutants of each species as,

$$s(\sigma_m, \sigma) = a(\sigma_m) - qN^*(\sigma, \rho) - b - \sigma_m\rho P^*(\sigma, \rho) \quad (13)$$

$$r(\rho_m, \rho) = c\sigma\rho_m N^*(\sigma, \rho) - d(\rho_m). \quad (14)$$

where $N^*(\sigma, \rho)$ and $P^*(\sigma, \rho)$ are the equilibrium densities for the resident populations. Considering the canonical Eq. (1) for a single trait, the canonical form of the coevolutionary dynamics is essentially a two-dimensional dynamical system, that is,

$$\frac{d\sigma}{dT} = \frac{1}{2}\mu_N\sigma_N^2 N^*(\sigma, \rho) \frac{\partial s}{\partial \sigma_m} \Big|_{\sigma_m=\sigma} \quad (15)$$

$$= \frac{1}{2}\mu_N\sigma_N^2 N^*(\sigma, \rho) [a'(\sigma) - \rho P^*(\sigma, \rho)] \quad (16)$$

$$\frac{d\rho}{dT} = \frac{1}{2}\mu_P\sigma_P^2 P^*(\sigma, \rho) \frac{\partial r}{\partial \rho_m} \Big|_{\rho_m=\rho} \quad (17)$$

$$= \frac{1}{2}\mu_P\sigma_P^2 P^*(\sigma, \rho) [c\sigma N^*(\sigma, \rho) - d'(\rho)]. \quad (18)$$

where μ_i and σ_i are the mutation rate and variance in mutation effect size for prey ($i = N$) and predators ($i = P$), respectively. It follows that any pair of traits (σ^*, ρ^*) where both selection gradients simultaneously vanish will be *co-singular strategies*. Crucially, while the mutation rates and population sizes (i.e., mutation supply) have no effect on the existence of co-singular strategies, they will affect both transient coevolutionary dynamics and the stability of any co-singular strategies. Evolutionary stability is unaffected by relative mutation rates and population sizes, as this is calculated for each species independently in the same way as for a single

evolving trait. Convergence stability is a bit more complicated, however, and requires consideration of the eigenvalues of the Jacobian matrix at a co-singular strategy:

$$J = \begin{pmatrix} \frac{1}{2}\mu_N\sigma_N^2 N^*(\sigma, \rho) \left[\frac{\partial^2 s}{\partial \sigma_m^2} + \frac{\partial^2 s}{\partial \sigma_m \sigma} \right] & \frac{1}{2}\mu_N\sigma_N^2 N^*(\sigma, \rho) \left[\frac{\partial^2 s}{\partial \sigma_m \rho} \right] \\ \frac{1}{2}\mu_P\sigma_P^2 P^*(\sigma, \rho) \left[\frac{\partial^2 r}{\partial \sigma \rho_m} \right] & \frac{1}{2}\mu_P\sigma_P^2 P^*(\sigma, \rho) \left[\frac{\partial^2 r}{\partial \rho_m^2} + \frac{\partial^2 r}{\partial \rho_m \rho} \right] \end{pmatrix}$$

The signs of the eigenvalues of this matrix tell us whether all nearby coevolutionary trajectories converge to a co-singular strategy (see (Marrow et al., 1996) for a detailed description of this approach). There are a couple of things of note in the matrix above. First, the terms on the main diagonal are the standard convergence stability terms if each trait were evolving in isolation, which Kisdi (2006) terms *isoclinic stability*. Second, the mutation supply for each population can have an effect on convergence stability, to the extent that a co-singular strategy may change from being locally attracting (i.e., a CSS or branching point) to locally repelling (i.e., a repeller or Garden of Eden) purely due to changes in relative mutation supply. Third, convergence stability is also affected by the cross-terms in the off-diagonal—that is the effect of each species on the other—meaning that one species can drive the other away from or towards its singular strategy. In sum, this means that to have convergence stability under coevolution, at least one of the traits must be convergence stable under one-sided adaptation (the main diagonal terms), but convergence stability of both traits under one-sided adaptation is neither sufficient nor necessary to have convergence stability under coevolution.

Although the situation is typically more complex under coevolution than under evolution, in cases where one species typically evolves much faster than the other (e.g., RNA viruses and mammalian hosts) it may be possible to approximate the coevolutionary dynamics using a second separation of timescales (Buckingham and Ashby, 2024). By assuming that one species rapidly reaches a singular strategy while the other experiences little evolutionary change, the two-dimensional trait space effectively collapses down to a single curve along which the coevolutionary trajectory is constrained (see Buckingham and Ashby (2024)).

It is worth noting that if only one species evolves we are limited to the four generic outcomes shown in Fig. 2. While these remain the only outcomes *locally* to a co-singular strategy, now that we are in two-dimensional trait space other global behaviours are possible. One new possible outcome is coevolutionary cycling, where the traits of the two species are constantly oscillating (effectively a coevolutionary *limit cycle*). While not technically new, we can also see repeated evolutionary branching in each species, leading to considerable diversity in traits. Again, this has been found in examples including host-parasite systems (Best et al., 2010).

Fluctuating Ecological Dynamics

So far, we have only considered scenarios where the ecological (population) dynamics converge to a stable equilibrium. This means that the mutant invasion fitness is a scalar value for any fixed set of parameters and trait values. It is easy to determine whether the mutant may invade or not (subject to stochasticity (Proulx and Day, 2002)). However, in nature population sizes may continually fluctuate rather than settle at an equilibrium. This can be due to extrinsic factors, such as seasonality, or intrinsic factors such as time delays in the life cycle of organisms (Best and Ashby, 2023). In such cases invasion fitness is no longer constant but will vary with time. If invasion fitness is sometimes negative and sometimes positive as the resident population fluctuates, how can we determine whether a mutant will successfully invade?

While it is often helpful for us to think of the mutant invasion fitness as being the mutant's growth rate, more precisely it is given by the *dominant Lyapunov exponent* (Metz et al., 1992). As it happens, for a simple single-species equilibrium model this is simply the per-capita growth rate, but for more complex models it is not so simple. In the case of a structured population, invasion fitness is given by the dominant eigenvalue of the Jacobian matrix of the mutant's invasion dynamics (or equivalently, a proxy for invasion fitness can be found using the next-generation method [Hurford et al., 2010]). In a system where the ecological dynamics fluctuate, invasion fitness is given by the *Floquet exponent* (Best and Ashby, 2023). With some mathematical liberty, this is essentially the corresponding term to the eigenvalue when populations are at equilibrium.

We can think of the Floquet exponent as creating an "envelope" for the mutant's invasion dynamics (Fig. 3). As a simple example, assume that we have population dynamics which can be written as

$$N(t) = \exp(\lambda t)(A + \cos(\omega t)). \quad (19)$$

The $A + \cos(\omega t)$ term gives regular oscillations between $A + 1$ and $A - 1$ with period $2\pi/\omega$. The amplitude of the population's oscillation is then bounded by the value of $\exp(\lambda t)$. A plot of these dynamics are shown in Fig. 3, with the "envelope" shown as dotted curves. If $\lambda < 0$, then over time $\exp(\lambda t)$ tends toward zero, and the population must also collapse towards extinction as the envelope shrinks. However, if $\lambda > 0$, as in the figure, then over time $\exp(\lambda t)$ grows, and the size of the population—while still oscillating—will grow on average as the envelope expands. Notice in particular that in this example the density initially decreases—a quick numerical check of the dynamics might wrongly conclude that the strain would die out.

More generally, it can be shown that in a fluctuating system the mutant dynamics can be written as

$$N_m(t) = \exp(\lambda t)X(t). \quad (20)$$

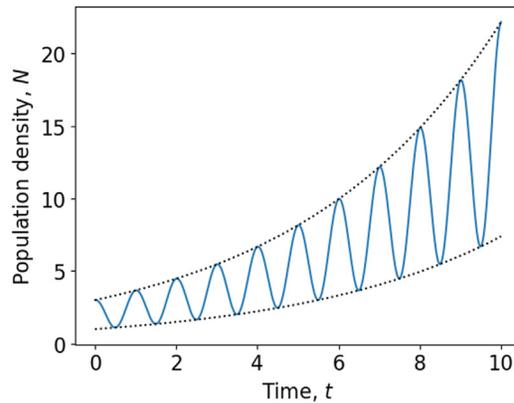


Fig. 3 Example time-course of a strain with fluctuating dynamics, given by Eq. (20). The dashed lines provide the “envelope” between which the strain’s population density is constrained. In this example, $\lambda = 0.2$, $A = 2$ and $\omega = 2\pi$.

Here, the function $X(t)$ may be extremely unpleasant and impossible to write down, but so long as it is bounded, this does not matter; it is the value of the exponent λ that determines whether the invasion of the mutant succeeds ($\lambda > 0$) or fails ($\lambda < 0$). Of course, this raises the obvious question of how to calculate λ . Some approaches have been developed in recent years, including cases where λ can be found analytically (Donnelly et al., 2013), constructing invasion fitness from contributions of mutant quality and quantity (Lion and Gandon, 2022) and numerical methods for finding λ (Best and Ashby, 2023).

Limitations and Alternative Approaches

Although Adaptive Dynamics is applicable to many biological scenarios, it has two major limitations. First, as a model of phenotypic evolution with quantitative traits, it cannot capture major gene effects among small numbers of loci and is therefore inappropriate for modelling scenarios where mutations have large, discrete effects or where genetic interactions due to dominance or epistasis are pronounced. Instead, it is generally better to model the combined density- and frequency-dependent dynamics of a finite number of alleles or genotypes using a system of ordinary differential equations or difference equations. However, in many cases, analytical tractability will be limited as a result of the high dimensionality that is typical of such systems.

Second, Adaptive Dynamics only focuses on long-term ecological and evolutionary outcomes and so is not suitable for capturing transient patterns of evolution. For example, during the early stages of an epidemic, when there is a plentiful supply of susceptible hosts, selection may favour higher transmissibility, but once immunity has accumulated in the population, selection may instead favour immune escape. Indeed, this pattern was observed during the Covid-19 pandemic, with early variants of concern (e.g., Alpha and Delta) typically having higher transmissibility than preceding variants, whereas the Omicron variant (and its subvariants) which arose later in the pandemic were characterised by their ability to evade naturally acquired and vaccine induced immune responses. Alternative methods that allow one to capture transient patterns of evolution while still accounting for eco-evolutionary feedbacks have been developed, such as applications using the Price Equation (Day et al., 2020) or “oligomorphic” dynamics (Sasaki and Dieckmann, 2011).

While these limitations are notable, it is often possible to combine analytic or numerical analysis based on the Adaptive Dynamics framework with simulations that relax key assumptions about the underlying genetics, strength of drift versus selection, and effect sizes of mutations or mutation rates. Simulations may be used to test the robustness of results to the key assumptions of Adaptive Dynamics.

Conclusions and Future Outlook

The Adaptive Dynamics framework is a valuable and widely applicable method for simultaneously modelling ecological and evolutionary dynamics and capturing important feedbacks between them. A key strength of the framework is its placement of ecology at the heart of evolution, with fitness derived from explicit ecological processes. As with any modelling framework, it has limitations which should be taken into consideration when formulating a model or interpreting the generality of results, in particular when mutations are common, have large effects, or when the focus is in short-term evolutionary dynamics. Several promising extensions of Adaptive Dynamics have recently been developed, especially to better capture short-term and non-equilibrium dynamics, and these are likely to be the focus of technical developments of the framework in the coming years.

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