

Adaptive Dynamics: Branching Phenomena and the Canonical Equation

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Abstract

In this paper we provide an introduction to the field of Adaptive Dynamics. We present derivations for two of the fundamental components of the theory: “canonical equation” and the classification of singular strategies. We supplement the existing theory with a derivation of the variance associated with the canonical equation. We then consider a common ecological model (an instance of the logistic equation) that has been used to explore branching in the context of Adaptive Dynamics. We show that the branching properties of this model are maintained in a much more general form of which the familiar example is a particular instance. We then determine the expected evolutionary trajectory of a population in this model using the canonical equation, and find the associated variance of this trajectory. We also examine the stability of the dimorphic, branched population. Having determined each of these components analytically, we then confirm these predictions by implementing a model using an individual-based stochastic simulation.

Chapter 1

Introduction

1.1 From Population Genetics to Adaptive Dynamics

The Modern Synthesis in the first half of the twentieth century served to unify Darwin's evolution with Mendel's genetics, providing a mechanism for natural selection to operate. The field emerging from this unification became known as population genetics, which experienced great success in several areas, such as an understanding under simple models how even very weak forces of natural selection could determine the evolution of large populations. However, the treatment of population genetics failed to account for ecological aspects of evolution, and consequently cannot provide an understanding of ecological aspects such as density and frequency dependent selection and their role in long-term evolution. Such considerations were first addressed through the techniques of mathematical game theory beginning in the 1970s [DOE Report, 2005]. Through this work the concept of an Evolutionarily Stable Strategy, ESS, (originally called an Evolutionarily Unbeatable Strategy, EUS) was developed [Metz *et al.*, 1996]. These game-theoretical techniques did not enable the classification of the dynamics of such points. The existence of such ESS did not guarantee that a population could ever reach such a strategy. This treatment has become the domain of a set of methods collectively known as Adaptive Dynamics [Geritz *et al.*, 1998, Dieckmann & Doebeli, 1999, Dieckmann & Law, 1996]. In this paper we provide an introduction to these techniques and illustrate their application to explore the phenomenon of branching in evolutionary populations, a question which serves as a paradigm with which to address one of the most interesting and challenging questions in long-term evolution: that of speciation.

Adaptive Dynamics offers an essentially analytic approach to the questions it seeks to address. Like most good theories, it makes certain simplifying assumptions and then employs a set of mathematical tools to explore the relevant questions. In population genetics, the assumptions simplify the ecology drastically, allowing for an explicit treatment of the genetics. Adaptive Dynamics works in

the other regime; trading genetic detail for ecological complexity [Dieckmann & Doebeli, 2005]. As such it is not a replacement for but rather an extension to the existing field. Such distinctions have been at the source of much recent controversy regarding the significance and role of Adaptive Dynamics. In light of what has largely been a controversy of misunderstanding [Kisdi & Gyllenberg, 2005], it is important to bear several distinctions in mind. The predictions made by theory are only valid inasmuch as the assumptions are satisfied, consequently we will state these assumptions as explicitly as possible. Further, one must keep the distinction between the set of tools and methods that comprise Adaptive Dynamics theory from the applications to particular ecological models. In this vein we begin by developing the abstract theory and follow with an example of its application. Finally, we employ the common practice of computer simulation to visualize the ecological model and the predictions made in our applications section. The practice has also contributed to some confusion in the literature, where such visualizations have been mistaken as the primary evidence of a particular result [Waxman & Gavrilets, 2005, Kisdi & Gyllenberg, 2005].

1.2 Fundamentals in Adaptive Dynamics

Our mission is to understand the evolution of a population in some ecological setting. This requires a model both for the ecology (population structure, growth, competition, and so forth) and a model for the evolution. Our objective is not to develop the most appropriate model for any of these aspects, but rather to develop a theoretical framework and set of techniques that can be applied to any particular model one might wish to investigate. Bearing this in mind, we construct a notation with which to address these questions, and then develop the tools we will later use to investigate a particular model of interest. First, the terminology and notation.

By population we imagine a group of individuals who can all be identified as having the same value for a particular trait, x .¹ Borrowing from the game-theory literature, we will consider this trait as the *strategy* employed by this population refer to them as x -strategists. This population may not be alone, but can be competing (or merely co-existing) with n other populations. We can then represent the strategies of each of these populations as elements of a vector, $\mathbf{X} = \{X_i\}_{i=1}^n$. Similarly, allow the vector $\mathbf{N} = \{N_i\}_{i=1}^n$ to represent the number of individuals practicing the corresponding strategy X_i . Finally, let us place our populations in some environment, $\mathbf{E}(\bar{N}, \bar{X}, t)$ that depends not only on external factors which may vary in time but on the strategies in play and the numbers of individuals practicing them.

¹We imagine this trait as some continuous variable $x \in \mathbb{R}$ that characterizes the population. There is no reason that this value must be positive; for instance the variable of interest may be the logarithm of the length. It is also possible to treat the trait values as functionals instead of real numbers, employing the calculus of variations. For simplicity we will continue to treat these values as real numbers.

Our initial question is how each strategy performs: that is, how does its population grow or shrink? We expect its average rate of growth to be proportional to its current size, that is,

$$\frac{dN_i}{dt} = s(X_i, \mathbf{E}(\mathbf{N}, \mathbf{X}, t)) \cdot N_i \quad (1.1)$$

Here $s(X_i, \mathbf{E})$ is the average rate of growth, which will depend on the strategy of the population in question $X_i = x$ and also on environmental factors, $\mathbf{E}(\mathbf{N}, \mathbf{X}, t)$, which of course include the effects of other populations. This results in the population growing (or shrinking) exponentially at rate $\rho(x, \mathbf{E})$. The exponential growth of N_i cannot be maintained indefinitely. As the population grows, it modifies the environment in a way which will cause its growth rate to deteriorate, reflecting limited resources, population density or other dependence that $\mathbf{E}(\mathbf{N}, \mathbf{X}, t)$ might have on \mathbf{N} . This causes the population to reach some equilibrium level which we denote as $N_i = N_i^*$. Clearly this will depend on the current environment which includes the traits and sizes of all other populations in the community. In the case of a monomorphic community (one where only a single strategy is being practiced) this population is obviously determined only by that strategy and the fixed environmental conditions. Under these conditions we will refer to the steady-state population size as being the carrying capacity, $K(x)$. In multi-strategy communities the steady-state populations can often be expressed as function of this inherent carrying capacity of the strategy in question and the influence of the other populations. We mention this for later reference, for now we continue to treat the general case of possibly polymorphic populations. Our first simplifying assumption is in regard to these equilibrium population sizes $N_x(x)$:

Assumption 1: Fluctuations in the steady state population size, $N_x(x)$ are negligible with respect to the dynamics. For instance, we won't worry about a population going extinct due to a chance fluctuation of low births and high deaths in one generation.

Note that the quantity $s(x, \mathbf{E})$ gives the expected exponential growth rate of a population, providing us with a precise and meaningful definition of the fitness of the species bearing trait x in the given environment \mathbf{E} . Our next assumption deals with this quality:

Assumption 2: $s(x, \mathbf{E})$ is a continuously smooth function of the x . Equivalently, small changes in phenotype x result in correspondingly small changes in the fitness s . This biological generality of this assumption has been challenged, see [Barton & Polechova, 2005].

We now build a mutation-based model of evolution upon this framework. Let μ represent the mutation probability per birth. In general this could depend on the trait value x , but for simplicity we will take this as constant for all possible trait values. The expected number of mutations per generation in a population N_i is then $\mu \cdot b(x) \cdot N_i$, where $b(x)$ is the birth rate per individual. When a mutant occurs, it carries a new trait y chosen from a normal distribution centered around a mean of x with variance σ_μ^2 . Here we introduce two critical assumptions of Adaptive Dynamics theory.

Assumption 3: $\mu \cdot \max(\mathbf{N}) \ll 1$. This assumption allows for the separation of timescales for evolutionary and ecological processes. Through this assumption we can assume that the mutant will occur in a population that has already equilibrated to steady state, \mathbf{E}_x . This steady state will depend not only on x , the trait value of that population, but on all other populations in the community (which may also need to be at equilibrium in order that population with trait x is at equilibrium).

Assumption 4: Mutants are nearly clonal offspring. This assumption together with assumption 1 will allow an approximation to s which we shall see shortly.

We are now prepared to consider what happens when a mutant first occurs in a population. Since individuals with the mutant trait are initially rare, their effect on the environment can be neglected. By assumption 3, the ecological dynamics of the population have equilibrated. From these two observations, we can write down the *invasion fitness* (growth rate) of the rare mutant y in a population of x as $s(y, E_x)$. To distinguish this as the invasion fitness, where y is rare, this is generally written in the literature as $s_x(y)$, which is read as the invasion fitness of y in a resident population of trait x . Here the dependence not only on the trait value from which the mutant originated (x) but on equilibrium environment E_x is implied by the subscript x . E_x of course depends on all other populations as well as a-biotic factors, allowing this more compact notion to remain completely general. Though we will not continue to write the E_x explicitly, we do not intend to suggest that we have abandoned a general treatment where the invasion fitness depends on environmental factors and any other resident populations.

By assumptions 1 and 3 we can approximate $s_x(y)$ by Taylor expanding around $y = x$,

$$s_x(y) \approx s_x(x) + D(x) \cdot [y - x] + \dots \quad (1.2)$$

Where

$$D(x) \equiv \left[\frac{\partial s_x(y)}{\partial y} \right]_{y=x} \quad (1.3)$$

By definition $s_x(x) = 0$. The mutant y can invade successfully when $s_x(y) > 0$. Hence if the invasion fitness gradient $D(x)$ is negative, only mutants with $y < x$ can invade, while if the gradient is positive, only those with $y > x$ will invade. As the population with trait y grows, we transition into an environment E_y where x is now rare. For nonzero $D(x)$ we will find $s_y(x) < 0$ and hence the mutant completely replaces the parent population². This results in the population climbing the gradient through successive mutations. Our first task

²This follows from assumptions 2 and 4. Because y is sufficiently similar to x (by assumption 4) the invasion fitness of x when rare will be close to that of the invasion fitness of y (by assumption 2). Being similar, the sign of the gradients $D(x)$ will not change once x becomes rare in a population of y ; that is when x and y are swapped in these equations. However the term $y - x$ will change sign, therefore $s_y(x) < 0$ as claimed. It is important to bear in mind that this is not the case in the region of a singular point where $D(x) = 0$. For further discussion see [Geritz *et al.*, 2002]

will be to describe the deterministic mean path of this stochastic trajectory. This is accomplished through the so-called canonical equation of Dieckmann and Law [Dieckmann & Law, 1996]. In addition to their classic derivation we will present a calculation of the variance associated with this mean trajectory.³ This trajectory may take the population to a value for X_i where $D(X_i) = 0$, and it becomes impossible to predict its evolution from the fitness gradient. We denote such a strategy $X_i = x^*$, which is termed an Evolutionarily Singular Strategy, or singular point. [Geritz *et al.*, 1998] We first derive the expected path to a singular strategy, and then consider their classification.

³I am unaware of such a calculation having yet appeared in the literature.

Chapter 2

The Canonical Equation

Our task here is to derive an equation giving the expected trajectory of an evolving population starting with a trait value $x_0 \neq x^*$ in some environment **E**. This is given by the canonical equation of Adaptive Dynamics, and was first derived in this context by Ulf Dieckmann and Richard Law [Dieckmann & Law, 1996]. Rather than direct the reader to this literature, we present the derivation as simply as possible employing the more familiar notation of S.A.H. Geritz [Geritz *et al.*, 1998] which we have been following thus far. The canonical equation gives the first moment (the mean trajectory) for this process. We follow up this classic result with a derivation of the second moment, allowing us to predict the variance in the trajectory of an evolving population from the mean trajectory given by the canonical equation.

2.1 The First Moment

We begin by observing that the trajectory of a population through the space of possible traits over time is Markovian, depending only on the current trait value of the population at time t . Consequently we can describe the evolution for the probability of the population having a particular trait value x at time t by the following master equation:¹

$$\frac{d}{dt}P(x, t) = \int dy [w(x|y) \cdot P(y, t) - w(y|x) \cdot P(x, t)] \quad (2.1)$$

Where $P(x, t)$ represents the probability of having trait x at time t while $w(y|x)$ gives the probability per unit time of making the transition $x \rightarrow y$. This transition probability consists of two events: (1) a mutant with trait y occurs in the population, with probability \mathcal{M} , and (2) the mutant survives accidental

¹The reader is directed to any text on stochastic processes for a discussion and derivation of this class of equations, e.g. van Kampen [van Kampen, 1981].

²Perhaps the most familiar example of these transition probabilities is that given by Fermi's Golden Rule, describing transitions of electrons between excited states of an atom.

extinction (drift), with probability \mathcal{D} . Since these processes are independent, the probability that both occur is simply their product:

$$w(y|x) = \mathcal{M}(y, x)\mathcal{D}(y, x) \quad (2.2)$$

The probability that a mutation enters a population is given by

$$\mathcal{M}(y, x) = \mu \cdot b(x) \cdot N_x(x) \cdot M(x, y - x) \quad (2.3)$$

Where $b(x)$ is the mean birth rate per individual, μ the mutation rate per birth, $N_x(x)$ the equilibrium population size for a population with trait x , and $M(x, y - x)$ is the distribution from which the mutant trait is drawn. Meanwhile, the probability of surviving drift given the mean individual birth rate b and mean death rate d for the mutant y is given by a classical result from branching process theory:

$$\mathcal{D}(y, x) = \begin{cases} \frac{b(y, x) - d(y, x)}{b(y, x)} & d(y, x) < b(y, x) \\ 0 & d(y, x) \geq b(y, x) \end{cases} \quad (2.4)$$

Where we use the notation of the dependencies, $b(y, x)$ to imply that this is the birth rate of a mutant with trait y in a population of x . The case of $\mathcal{D} = 0$ being trivial, we will focus only on the case where $d(y, x) < b(y, x)$. The derivation of this result can be found in any text on branching processes, e.g. [Feller, 1968]. Following equation (2.2) and simplifying, we have

$$w(y|x) = \mu \cdot N_x(x) \cdot b(x) \cdot M(x, y - x) \cdot [b(y, x) - d(y, x)]/b(y, x) \quad (2.5)$$

We can simplify this further by means of a convenient approximation. Taylor expanding $\mathcal{D}(y, x)$ about $y = x$, noting that $b(x, x) - d(x, x) = 0$:

$$\mathcal{D}(y, x) = [b(y, x) - d(y, x)]/b(y, x) \approx \frac{\partial_y [b(y, x) - d(y, x)]|_{y=x}}{b(x, x)} \cdot [y - x] \quad (2.6)$$

Where $b(x, x) = b(x)$, the birthrate of an x strategist in a population of x being by definition $b(x)$. The quantity $b(y, x) - d(y, x)$ is simply the expected growth rate, our familiar $s_x(y)$. Recall that from equation (2.4) that $\mathcal{D} \geq 0$, and consequently we have the condition that $\partial_y s_x(y)|_{y=x}$ and the quantity $[y - x]$ must have the same sign. Not coincidentally, this is identically the condition for invasion we determined in discussing the invasion fitness gradient $D(x)$ in equation (1.3). We can then express the transition probability as:

$$w(y|x) = [y - x] \cdot \mu \cdot N_x(x) \cdot M(x, y - x) \cdot \partial_y s_x(y)|_{y=x} \quad (2.7)$$

We are now ready to consider the dynamics of the expected trait value:

$$\frac{d}{dt}\langle x \rangle(t) = \int dx \cdot x \cdot \frac{d}{dt}P(x, t) \quad (2.8)$$

Using the master equation to replace $\frac{d}{dt}P(x, t)$ and performing a change of variables we find

$$\frac{d}{dt}\langle x \rangle(t) = \int dx \int dy \cdot [y - x] w(y|x) P(x, t) \quad (2.9)$$

defining the k th jump moment [van Kampen, 1981]³ as

$$a_k(x) = \int dy \cdot [y - x]^k w(y|x) \quad (2.10)$$

We then have

$$\frac{d}{dt}\langle x \rangle(t) = \int dx \cdot a_1(x) P(x, t) = \langle a_1(x) \rangle(t) \approx a_1(\langle x \rangle(t)) \quad (2.11)$$

Which tells us that the quantity we seek is just the expectation value of the first jump moment, $\langle a_1(x) \rangle(t)$. If $a_1(x)$ is linear, we could take $\langle a_1(x) \rangle = a_1(\langle x \rangle)$. In general this will not be true, and we would instead write

$$\langle a_1(x) \rangle \approx a_1(\langle x \rangle) + \frac{1}{2} \langle (x - \langle x \rangle)^2 \rangle a_1''(\langle x \rangle) + \dots \quad (2.12)$$

Hence the evolution of $\langle x \rangle$ is not determined only by $\langle x \rangle$ but is also influenced by its fluctuations. The statement that we will ignore the fluctuations is exactly what we do when we consider any macroscopic quantity that results from stochastic fluctuations, such as chemical rate constants or Ohm's law. We desire to describe the world in terms of these macroscopic quantities alone, when a precise description should depend not only on these values but on their fluctuations. The assumption that the macroscopic quantity is by itself a meaningful description of the phenomenon (without reference to its variance) is the assumption that the second term in this approximation is negligible. N.G. van Kampen describes this as the *macroscopic approximation*. With regard to the process considered here, Dieckmann and Law simply refer to van Kampen for a justification of this approximation for nonlinear a_1 . While this approach will provide an accurate description of the mean path, it gives no such justification as to whether the mean path is a meaningful macroscopic quantity analogous to the resistance of a wire. With this precaution, we continue:

Using equation (2.7) in equation (2.10) we have:

$$\frac{d}{dt}\langle x \rangle(t) = \int dy \cdot [y - x]^2 \mu N_x(x) M(x, y - x) \partial_y s_x(y) \Big|_{y=x} \quad (2.13)$$

We now change our integration variable to $\Delta x \equiv y - x$. Since we have the condition on (2.4) that $[y - x]$ is either always positive or always negative, we must restrict our range of integration to half of the real line. Since M is

³van Kampen introduces this term for this concept in place of an earlier term, "derivative moment," which never became established. Unfortunately, van Kampen's term does not seem to have established itself much beyond Dieckmann and Law. Nevertheless, we shall see that the concept is quite powerful.

symmetric and the only function depending on Δx , we can equivalently integrate over all of \mathbb{R} and introduce a factor of $1/2$,

$$\frac{d}{dt}\langle x \rangle(t) = \frac{1}{2} \cdot \mu \cdot N_x(x) \cdot \partial_y s_x(y)|_{y=x} \cdot \int d\Delta x \cdot \Delta x^2 M(x, y-x) \quad (2.14)$$

The remaining integral we recognize simply as the variance in M , the distribution from which the mutational trait is drawn. Denoting this integral simply σ_μ^2 we recover the canonical equation:

$$\boxed{\frac{d}{dt}\langle x \rangle(t) = \frac{1}{2} \cdot \mu \cdot \sigma_\mu^2 \cdot N_x(x) \cdot \partial_y s_x(y)|_{y=x}} \quad (2.15)$$

2.2 The Second Moment

Along these same lines, it is possible to derive the variance expected for this mean path. Analogously to before, we have the identity

$$\begin{aligned} \frac{d}{dt}\langle x^2 \rangle(t) &= \int dx \int dy \cdot [y^2 - x^2] w(y|x) P(x, t) \\ &= \int dx \int dy \cdot [[y - x]^2 + 2x[y - x]] w(y|x) P(x, t) \\ &= \langle a_2(x) \rangle(t) + 2\langle x a_1(x) \rangle(t) \end{aligned}$$

Recall the variance is given by $\sigma^2(t) = \langle x^2 \rangle(t) - \langle x \rangle^2(t)$. Differentiating with respect to time, we have

$$\frac{d\sigma^2}{dt} = \langle a_2(x) \rangle(t) + 2\langle [x - \langle x \rangle(t)] a_1(x) \rangle(t) \quad (2.16)$$

Then with the assumption of linearity for both jump moments and expanding a_1 around $x = \langle x \rangle$, we can write:

$$\boxed{\frac{d\sigma^2}{dt} = a_2(\langle x \rangle(t))(t) + 2\sigma^2 a_1'(\langle x \rangle(t))} \quad (2.17)$$

This gives us the variance associated with the canonical equation. Clearly the second jump moment is always positive. Meanwhile in order for equation (2.15) to approach equilibrium a_1' must be negative near the equilibrium point. Consequently we expect σ^2 will converge towards a steady state of

$$\sigma^2 = \frac{a_2}{2|a_1'|} \quad (2.18)$$

Hence the variance will grow initially but does not continue to diverge, instead settling in towards a maximum value. This provides a valuable measure of the accuracy of the canonical equation for any particular instance. Further,

this allows us to add a correction to the canonical equation itself. So far we have written the canonical equation as $\langle \dot{x} \rangle = a_1(\langle x \rangle)$. Under the expansion in (2.12) we could instead write

$$\langle \dot{x} \rangle = a_1(\langle x \rangle) + \frac{1}{2} \sigma^2 a_1''(\langle x \rangle) \quad (2.19)$$

This is currently rather abstract and will hopefully become clearer when we compute these quantities for a particular model of interest in a later section.

Chapter 3

Singular Strategies

Through our derivation of the canonical equation we have reached an expression describing the average trajectory of a population across a fitness gradient. When a population has reached the singular strategy, x^* , the gradient $D(x)$ can no longer tell us about the dynamics; we must consider higher terms in our expansion of the invasion fitness, equation (1.2). We will show that any singular point can be divided into one of eight categories on the basis of its second derivatives. The discussion here is intended to be self contained but not expansive. For a more thorough treatment see [Geritz *et al.*, 1998].

Our first consideration is to establish whether or not the singular point is evolutionarily stable. To determine if a mutant can invade a population with strategy x^* (that is, $s(y, x^*) > 0$) we simply continue our expansion in equation (1.2) to second order:

$$s_x(y) \approx s_x(x) + [y - x] \left[\frac{\partial s_x(y)}{\partial y} \right]_{y=x=x^*} + [y - x]^2 \left[\frac{\partial^2 s_x(y)}{\partial y^2} \right]_{y=x=x^*} \quad (3.1)$$

Since the first term vanishes by definition as before, and the gradient is zero by definition at x^* , we are left with the following condition for mutant of some nearby strategy y to be able to invade a population with strategy x^* :

$$B \equiv \left[\frac{\partial^2 s_x(y)}{\partial y^2} \right]_{y=x=x^*} > 0 \Leftrightarrow x^* \text{ is invisable} \quad (3.2)$$

Considering the sign of the second derivative offers another way to think about the question. For $B < 0$, the invasion fitness landscape $s_x(y)$ has a local maximum with respect to y at the critical point, (x^*, x^*) . Since $s(x^*, x^*) = 0$ by definition, this means that all nearby values for y have negative invasion fitness, $s(y, x^*) < 0$, and hence none of them can invade x^* . This means x^* is uninvasible, and consequently acts as an evolutionary trap: any population with strategy x^* will never be ousted by its mutants. This does not tell us anything about the dynamics in general however. Whether a population with a strategy

initially different from x^* could ever reach the strategy x^* is an independent question. This is one of the key distinctions that Adaptive Dynamics adds to the game-theoretical concept of evolutionarily stable. We will see that even if x^* is uninvadable, it may be impossible for a population to reach the strategy x^* by evolution.

For instance, we must first ask: can a rare mutant with strategy $y = x^*$ invade a nearby population with strategy x ? Mathematically, to invade x^* needs a positive invasion fitness, $s(y = x^*, x) > 0$. This time we expand around the second variable, taking the resident population x near the fixed value of $y = x^*$,

$$s_x(y = x^*) \approx s_{x^*}(x^*) + (x - x^*) \left[\frac{\partial s_x(y = x^*)}{\partial x} \right]_{x^*=x} + \frac{(x - x^*)^2}{2} \left[\frac{\partial^2 s_x(x^*)}{\partial x^2} \right]_{x=x^*} \quad (3.3)$$

The first term $s_{x^*}(x^*)$ and the first derivative term are again zero for the same reasons. Again we are left with the sign of the second derivative giving us the sign of the invasion fitness $s_x(y = x^*)$. A positive invasion fitness for rare x^* corresponds with the invasion fitness landscape having a local minimum with respect to x . Recalling that $s_{x^*}(x^*)$ is zero, we see that for any x near x^* , the strategy has a positive invasion fitness and hence when rare. Our condition that x^* strategists can invade is thus

$$A \equiv \left[\frac{\partial^2 s_x(y)}{\partial x^2} \right]_{y=x=x^*} > 0 \Leftrightarrow x^* \text{ can invade} \quad (3.4)$$

Note that this condition is completely independent of our first condition. One could have a singular point for which any population beginning with the value x^* would be stable, but even populations beginning very close to the point could never reach. Even if we know that x^* is uninvadable (when established) and can invade nearby populations (when rare), we still know nothing about its global stability; that is, whether a population with a strategy initially far from x^* will converge towards it or away from it. Since the population moves along the fitness gradient, this requires that $s_x(y) > 0$ for y nearer x^* than x and conversely, $s_x(y) < 0$ for $|x^* - y| > |x^* - x|$. Since $D(x)$ changes sign at x^* , this requires that $D(x)$ be a decreasing function of x , that is,

$$\frac{dD(x)}{dx} = \frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} < 0 \quad (3.5)$$

Where we have expanded the full derivative of $D(x)$ (from equation (1.3)) in terms of the second partials. Recall that since the average rate of growth for a steady state population must be zero, $s(y = x, x) = 0$. Consequently, any derivatives of $s_x(y)$ along the line $y = x$ direction must be zero. Expanding the second derivative along this line we find:

$$\frac{\partial^2 s_x(y)}{\partial x^2} + 2 \frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} = 0 \quad (3.6)$$

Which we use to replace the mixed partial in equation (3.5), giving us the condition

$$\frac{\partial^2 s_x(y)}{\partial x^2} - \frac{\partial^2 s_x(y)}{\partial y^2} > 0 \Leftrightarrow x^* \text{ is convergence stable} \quad (3.7)$$

Following our definitions of A and B (equations (3.4) and (3.2)) we can write the convergence stability condition simply as $A - B > 0$. Finally, we have observed that whether x^* can invade when rare is independent of whether x^* can be invaded when common. Hence around the critical point it is possible for both $s(y, x^*) > 0$ (x^* invasible by nearby mutants) and $s(x^*, x) > 0$ (x^* can invade nearby populations). In this case neither can replace the other, and the population must become dimorphic. In general this requires the invasibility to appear the same when we swap y and x , that is, reflect across the line $y = x$ in the invasion landscape. Hence the strategies to be mutually invasible $s_x(y)$ must have a minimum in the direction perpendicular to $y = x$,

$$\frac{\partial^2 s_x(y)}{\partial x^2} - 2 \frac{\partial^2 s_x(y)}{\partial x \partial y} + \frac{\partial^2 s_x(y)}{\partial y^2} > 0 \quad (3.8)$$

Using this to replace the mixed partial in equation (3.5), we have the condition

$$\frac{\partial^2 s_x(y)}{\partial x^2} + \frac{\partial^2 s_x(y)}{\partial y^2} > 0 \quad (3.9)$$

Which is simply the condition $A + B > 0$ for polymorphisms to be protected. Clearly our last two conditions are not independent, but amount to the question of whether $|A| - |B| > 0$. Any singular point could have any combination for the sign of A , B , and $|A| - |B|$, making for a total of eight unique types of critical points. It is possible to make a simplified sketch of these invasion fitness landscapes as follows. Imagine that we have a topographic map with values of x along the abscissa, values of y along the ordinate, and the corresponding value $s_x(y)$ as the height of that point on the map. Clearly along the line $y = x$ the height is zero, or sea-level. Rather than worry about the exact value of $s_x(y)$ everywhere, we simply color in the areas on this map lying above sea-level. This is called a pairwise invasibility plot, and are discussed in greater detail in [Geritz *et al.*, 1998]. See figure 3.1 and figure 3.2 as examples.

The critical point in which each of these signs is positive is particularly interesting. Such a point is convergence stable, invasible, able to invade, and permits polymorphisms. Any point satisfying these criteria is known as a branching point, since a monomorphic population beginning anywhere in the trait space will necessarily branch into populations with different traits. Our study of diversification in asexual populations will require a dynamics satisfying these criteria for branching. Having characterized the behavior of the singular points by means of these four properties, we turn our attention to describing the dynamics of a population evolving away from a critical point; that is, when the selection gradient is nonzero.

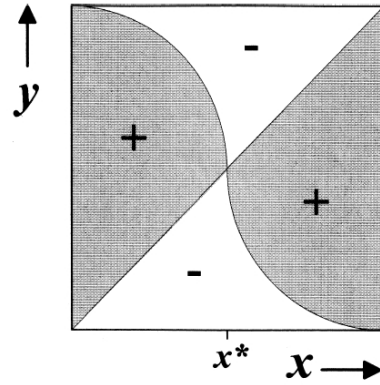
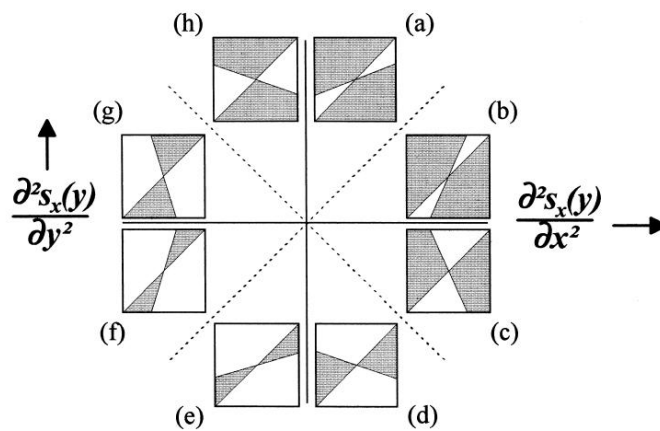


Figure 3.1: Sample pairwise invasibility plot (PIP). A population must start on the line $y = x$ at equilibrium. It can then take a small mutational step along the vertical (along the ordinate) direction into any positive region. These mutants then successfully invade, carrying the population horizontally (along the abscissa) back to the line $y = x$. This PIP exhibits a singular point at $x = x^*$ and represents an uninvadable (evolutionarily stable) strategy. Figure reproduced from [Geritz *et al.*, 1998].



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Chapter 4

Applications to a Branching Equilibrium Example

4.1 Generalizing a Common Branching Model

We now turn to consider a particular example which will serve to illustrate these techniques and also allow us to explore the phenomenon of branching populations. Dieckmann and Doebeli consider a classic form for ecological dynamics that exhibits branching in the paper on speciation [Dieckmann & Doebeli, 1999]. We demonstrate that the properties of the model they consider are in fact preserved by a more general class of such models. This derivation serves as an illustration of the methods outlined in the previous section and also as a demonstration that these models feature the branching property we wish to explore. We write down our general form for these models as:

$$\frac{d\mathbf{N}(x, t)}{dt} = [b(x, \mathbf{N}) - d(x, \mathbf{N})]\mathbf{N}(x, t) \quad (4.1)$$

Where b represents a generalized birth rate and d a generalized death rate. The motivation for this formulation is then clear: the population is expected to grow exponentially at the net rate at which individuals enter the population (births minus deaths). These rates are allowed to depend on the particular trait value (the so-called strategy, x) of the population in question. We assume the following general forms for birth and death as linear functions of the population:

$$b(x, t) := \nu(x) - \beta(x)\mathbf{N}(x, t), \quad d(x, t) := \rho(x) + \alpha(x)\mathbf{N}(x, t) \quad (4.2)$$

Clearly, the steady state occurs when $b(x) = d(x)$. That is, when

$$\nu(x) - \beta N_x(x) = \rho(x) + \alpha N_x(x) \quad (4.3)$$

Where N_x indicates the steady state population as before, which we will identify as the carrying capacity $K(x)$ of some fixed environment. Solving for this we find:

$$N_x = \frac{\nu(x) - \rho(x)}{\alpha(x) + \beta(x)} = K(x) \quad (4.4)$$

We will assume that this carrying capacity is also a Gaussian, offering the maximum capacity K_0 for some optimal trait x^* .

$$K(x) = K_0 e^{-(x-x^*)^2/(2\sigma_k^2)} \quad (4.5)$$

The only necessary features for $K(x)$ in our derivation will be $K(x^*) = K_0$, while $K'(x)|_{x=x^*} = 0$ and $K''(x)|_{x=x^*} < 0$. We now consider the per capita growth rate of the rare mutant¹. We will assume that the rare mutant competes against a discounted population size, weighted by how similar the mutant is to the population it invades. This weighting we will denote by $C(x-y)$ indicating that it depends only on how different two populations in the community are, not on the values themselves. This $C(x-y)$ is called the competition kernel, and is conventionally taken to be a simple Gaussian centered at the trait itself.

$$s_x(y) = [\nu(y) - \rho(y)] - [\alpha(y) + \beta(y)]N(x)C(x-y) \quad (4.6)$$

Where $C(x-y)$ has the explicit form:

$$C(x-y) = \exp(-(x-y)^2/(2\sigma_c^2)) \quad (4.7)$$

As with $K(x)$, we will only be interested in the values this function and its derivatives takes at the critical point, not the actual form. Given equation (4.6), we are ready to apply the machinery we have developed into identifying and classifying the equilibrium point. These derivations are carried out explicitly in the appendix, and the main results quoted here. Not surprisingly, we find the equilibrium condition to be x^* . We find the condition for x^* to be able to invade as:

$$\partial_x^2 s_x(y) \big|_{y=x=x^*} = \frac{K_0[\alpha(x) + \beta(x)]}{\sigma_k^2} + \frac{\nu(x) - \rho(x)}{\sigma_c^2} \bigg|_{x=x^*} \quad (4.8)$$

Which is clearly always greater than 0 (given $\forall x \quad \nu(x) - \rho(x) > 0$), hence x^* can always invade. Our next condition is that x^* is invisable,

$$\frac{\nu(x) - \rho(x)}{\sigma_c^2} - \frac{K_0[\alpha(x) + \beta(x)]}{\sigma_k^2} \bigg|_{x=x^*} \quad (4.9)$$

Which is only positive for $\sigma_k > \sigma_c$, making this a necessary requirement for branching to occur. Our condition for protected polymorphisms is similarly always satisfied, as the sum of these is always positive:

$$[\partial_x^2 s_x(y) + \partial_y^2 s_x(y)]_{x=y=x^*} = \frac{2[\nu(x) - \rho(x)]}{\sigma_c^2} \bigg|_{x=x^*} \quad (4.10)$$

¹were the mutant not rare, the second term would be $[\alpha y + \beta(y)]N(x)C(x-y) + N(y)$, but since the mutant is rare $N(y) \approx 0$.

Finally, our condition that x^* is convergence stable, requires the difference to be always positive:

$$[\partial_x^2 s_x(y) + \partial_y^2 s_x(y)]_{x=x^*} = \frac{2K_0[\alpha(x) + \beta(x)]}{\sigma_k^2} \quad (4.11)$$

This leaves us with the sole condition $\sigma_k > \sigma_c$ for x^* to be a branching point. If the inequality is reversed, a population will converge to x^* , rare mutants with the strategy x^* will then emerge and successfully invade, and the population will remain stably at x^* despite invasion attempts by nearby mutants. Note that only each of these steps are satisfied by independent conditions, and only the last does not hold in the case of branching.

4.2 Predicting Dynamics in Evolutionary Branching

Having shown that we obtain a branching point for the general form of the logistic equation given in (4.1), we will now assume an explicit form so that we can explore the dynamics more closely. Matching the landmark paper on evolutionary branching in Adaptive Dynamics by Dieckmann and Doebeli [Dieckmann & Doebeli, 1999], we take the the following assignments for equations (4.2): $\nu(x) = r$, $\beta = 0$, $\rho(x) = 0$, and $\alpha = \frac{r}{K(x)}$ we can write our invasion fitness (equation (4.6)) as:

$$s_x(y) = r - \frac{r \sum_i^n N(x_i) C(x_i - y)}{K(y)} \quad (4.12)$$

We assume the same form for $K(x)$ and $C(y - x)$ as specified in equations (4.5) and (4.7). As this is of the general form discussed above, we have already shown that this model will have a branching point at x^* . Having determined that our species will branch, we now ask what happens next? We assume that the branching initially results in two populations of equal sizes symmetrically spaced about x^* (which for convenience is taken to be at $x^* = 0$), and applying the techniques we have discussed, (see appendix (B) for the calculations) we find that two new single points exist, symmetrically spaced at:

$$x = \pm \left[\frac{\sigma_c^2}{2} \log \left(\frac{2\sigma_k^2 - \sigma_c^2}{\sigma_c^2} \right) \right]^{\frac{1}{2}} \quad (4.13)$$

Similarly we can evaluate the stability of these points. Somewhat surprisingly² Taking the second derivative of the invasion fitness (4.12) and evaluating at the branching points above we find (see appendix (B)):

$$\frac{-2\sigma_k^4 + 4\sigma_k^2 x^2 + 2\sigma_c^2(\sigma_k^2 - x^2)}{\sigma_c^2 \sigma_k^2 (\sigma_c^2 - 2\sigma_k^2)} \quad (4.14)$$

²Dieckmann and Doebeli give no indication that these points are unstable, suggesting that this simply results in two new species [Dieckmann & Doebeli, 1999].

This term is always positive for $\sigma_k > \sigma_c$, even when σ_k gets arbitrarily close to σ_c (see appendix (B)). Consequently this point is always unstable and result in subsequent branching. This prediction is explored in more depth through simulation.

Meanwhile, we can also derive the expected trajectory for a monomorphic population starting far from the critical point using the canonical equation, (2.15). We evaluate the fitness gradient,

$$\partial_y s_x(y)|_{y=x} = \frac{-r[x - x^*]}{\sigma_k^2} \quad (4.15)$$

Further, recall that for a monomorphic population the equilibrium population size is the carrying capacity associated with that trait, $N_x(x) = K(x)$. Hence we have

$$\frac{d}{dt}\langle x \rangle(t) = a_1(\langle x \rangle) = -\frac{1}{2}r\mu\sigma_\mu^2 K(x) \frac{-[x - x^*]}{\sigma_k^2} \quad (4.16)$$

As the carrying capacity depends on x , we will integrate this numerically to obtain the expected trajectory.

Similarly, we can find the variance associated with this on the basis of equation (2.17). If we first calculate the second jump moment using the same approximation as before,

$$\langle a_2 \rangle(t) = \int dy \cdot [y - x]^3 \mu N_x(x) M(x, y - x) \partial_y s_x(y)|_{y=x} \quad (4.17)$$

We immediately see that for our Gaussian M that this vanishes. Since the steady state variance depend on this term, we need to revisit the approximation we made in equation (2.6), carrying it out to higher order than we had to merely to obtain the canonical equation originally. In doing so we will make use of the fact that in our model birth rates are constant. We have also already substituted in for the invasion fitness, $b(y, x) - d(y, x) = s_x(y)$.

$$\mathcal{D}(y, x) \approx \frac{\partial_y [s_x(y)]_{y=x}}{b(x, x)} [y - x] + \frac{\partial_y^2 [s_x(y)]_{y=x}}{b(x, x)} [y - x]^2 \quad (4.18)$$

Note that this will not actually change the first jump moment, since we see by equation (2.10) that the new term will result in being the third moment of $M(x, y - x)$ in a_1 , which vanishes as we have just seen. Meanwhile, by equation (2.10) we now obtain the fourth moment of $M(x, y - x)$ in our expression for a_2 ,

$$a_2 = \mu K(x) \partial_y^2 [s_x(y)]_{y=x} \int d\Delta x \cdot \Delta x^4 M(x, \Delta x) \quad (4.19)$$

Evaluating the integral and the derivatives we recover³

$$a_2 = 3r\mu\sigma_\mu^4 K(x) \left[\frac{1}{\sigma_c^2} - \frac{1}{\sigma_k^2} \right] \quad (4.20)$$

Returning to our first jump moment and taking the derivative with respect to x we have,

$$\frac{d}{dx}a_1(x) = \frac{1}{2} \frac{r\mu\sigma_\mu^2}{\sigma_k^2} \left[\frac{[x - x^*]^2}{\sigma_k^2} - 1 \right] K(x) \quad (4.21)$$

Putting this into equation (2.17) gives us our differential equation for the variance as a function of time.

We now turn from our analytical treatment of this well-known ecological model to computer simulation in order to confirm our predictions and further explore the dynamics.

4.3 A Simulation-based Test of Theoretical Predictions

We design an individual-based simulation for the model given by equation (4.12). We employ an event driven approach which offers an exact simulation for stochastic processes known as Gillespie's algorithm [Gillespie, 1977]. Using this model we can simulate equation (4.12) and evaluate the predictions we derived from it. Parameter values for the simulations are given in table 4.1. Code is provided in Appendix C for reference.

4.3.1 Confirming Branching

Our model provides a clear example of an evolutionary branching point for $\sigma_k > \sigma_c$, as seen in simulations such as figure 4.1. Our analysis predicts that a monomorphic population starting some distance from the singular point will converge towards the singular point while remaining essentially monomorphic (consisting of only a growing mutant population and the dying resident population) until it reaches the vicinity of the singular point. At this point, the further mutations lead to the population branching into two distinct populations, as seen in figure 4.1(a).

It is possible to confirm that the model is in the regime specified by assumption 3 (that the mutation rate is low enough to allow for equilibration)

³A close look at this equation reveals that it becomes negative for values of x larger than some value (for which there is no simple analytical representation but can easily be determined numerically). This is contrary to the definition of a_2 given by equation 2.10 and consequently must be an artifact introduced by the approximations made. Simply expanding (2.6) to higher orders is however insufficient to guarantee that a_2 is always positive for this particular formulation of $s_x(y)$. We do not have space to explore this issue further within the confines of this paper, and it is thus left as an observation open to further investigation. We note that this effectively gives a parameter range of starting conditions for which this expression works.

Parameter	symbol	value
Mutation rate per birth	μ	0.001 *, 0.0001 **
Variance in mutation values	σ_μ	1/20
Variance for Carrying Capacity, $K(x)$	σ_k	1
Variance of Competition kernel, $C(x - y)$	σ_c	.4
Maximum of Carrying Capacity	K_0	500 *, 5000 **
Value of singular point strategy	x^*	0
Starting population trait	x_0	1, 0, .9 †

Table 4.1: * Values for figure 4.1(a) and 4.2. ** Values for figure 4.1(b). † Values for figure 4.1(a), 4.1(b), and 4.2 respectively. All other values universal to all simulations.

by observing that populations do indeed grow to their equilibrium sizes before mutants from that population start to grow into new populations. When this assumption is violated, the population need not converge while remaining monomorphic. Instead, when a resident population gives rise to mutants, those mutants generate further mutants before the resident population can go extinct. In this regime populations still converge to the singular point and branch, but always with this higher level polymorphisms due to the multiple mutants. As this lies outside the realm of adaptive dynamics proper we merely provide this observation as a caution regarding the simulation parameters employed.

In our calculations we demonstrated that though this initial branching results in two distinct populations spaced some distance from the equilibrium population, these points are in fact unstable. We further explore this instability by running the simulations long enough to see the repeated branching.

4.3.2 The Instability of Branching

The instability of the initial branching event is somewhat surprising in light of the treatment this particular ecological model receives within the literature. The simulations suggest that it is not merely this first branching that is unstable, but that these points result in further divisions. It is unclear that this should have any direct connection to period doubling bifurcations of chaotic systems. For instance, the subsequent branching of the original two branches need not occur at the same time. Not only is this a consequence of the stochastic nature of the simulation, but that the branching of one effects the other, changing the position of the singular point.

Equation 4.13 predicts the location of the first branching, given that the branching occurs symmetrically. While this condition need not be satisfied, nevertheless our expression usually approximates well the location of the first subsequent branching. We do not yet have sufficient data to determine if this branching process continues or stabilizes after a finite number of branchings. These features can be seen in figure 4.1.

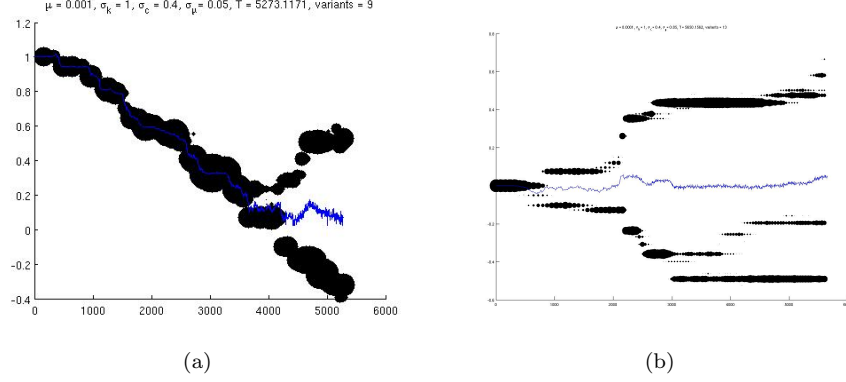


Figure 4.1: Population branching: Figures show time on the abscissa and trait value on the ordinate. Population size is indicated by the size of the dot. Particular parameter values used in each simulation are given at the top of each graph. (a) A population starting initially at some distance away from the branching point converges towards it and then begins to branch. (b) A population undergoes successive branching. The blue curve is the weighted mean trait value. Note that for the parameters illustrated here, the symmetric critical points, equation (4.13), occur at ± 0.44 , roughly agreeing with the onset of the first subsequent branching.

4.3.3 Evaluating the Canonical Equation and its Variance

Integrating the canonical equation for this system, equation (4.16), we can predict the mean trajectory of a monomorphic population starting some distance from the singular point. In order to compare our prediction with the data, we must first collect enough samples to have a reliable measure of the actual mean path. Additionally we can integrate the variance equation (2.17), using the jump moments we calculated in (4.20) and (4.21). As seen in figure 4.2, the match of both the canonical equation and the variance to the simulation data is rather good. The correction that we calculated to the canonical equation given by equation 2.19, accounting for the variance dependence of the mean, is also plotted, and shows a small but noticeable improvement in predicting the mean path. The simulation is run in a regime such that most trajectories will not actually reach the branching point and begin to branch, since this behaviour is no longer described by the canonical equation.

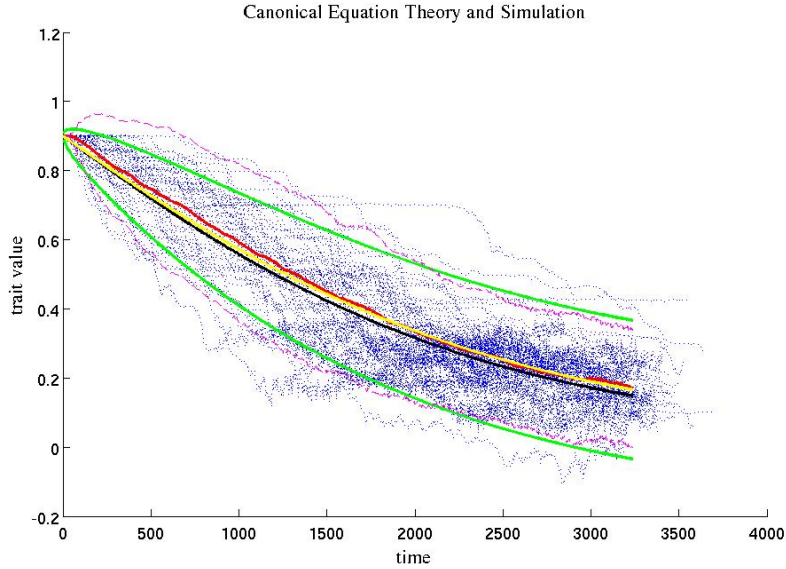


Figure 4.2: Confirming the canonical equation and its associated variance relation: The simulation is run for a fixed number of events with a single population starting at a set distance (.9) from the singular point. The plot shows time on the abscissa and trait value on the ordinate, as in figure 4.1. The blue curves show the weighted mean trait values for each run. The red curve gives the mean path (average of the blue curves). Dashed pink curves are give the standard deviation of the paths. The black curve is the canonical equation, numerically integrated, which lies very close to the mean path. The yellow curve is the canonical equation with the correction discussed in the text, which offers a small but noticeable improvement relative to the fit of the original canonical equation of Dieckmann and Law (black curve), [Dieckmann & Law, 1996]. The solid green curves give the standard deviation calculated in the text (integrated numerically), which also appears to agree reasonably well with the actual variance in these 50 runs.

Chapter 5

Conclusions

In this paper we have introduced the basic concepts of Adaptive Dynamics theory and derived its fundamental results: the canonical equation and the classification of singular points. In addition, we have added a derivation of the variance associated with the canonical equation, which we showed can also be used to provide a correction to the canonical equation of the mean. We showed that the properties of a model for a branching singular point that is commonly used in the literature hold for a more generalized form. Using the common model as a particular instance of such a branching singular point, we applied the canonical equation and the associated variance equation to this model when a monomorphic population begins far from the critical point. We confirmed these predictions through stochastic simulation. We also perform stability analysis to the model where two populations have branched off from the critical point, determining that these branches are unstable. The stochastic simulation confirm that following the initial branching event, the populations continue to branch.

Several interesting possibilities remain for further exploration. The limit of continual branching could be explored further through simulation, and one may also be able to analytically prove no stable configuration of finite n branches exists. Using the same model for $\sigma_k < \sigma_c$, the singular point becomes evolutionarily stable, and remains able to invade, remains convergence stable and still features protected polymorphism. The dynamics associated with polymorphisms in this case would be rather different than the branching case, and may be interesting to explore further. One could also explore the effects of using functions other than Gaussians that still satisfy the criteria for branching outlined in the generalization section. Though the timescale of the initial relaxation to the equilibrium point for a monomorphic population is given by the canonical equation, no similar characterization exists for the timescale of the branching events. Presumably this could be explored analytically in a similar vein, and it could certainly be explored in further simulation. Similarly, it may be interesting to study the canonical equation's relaxation prediction in the event of polymorphic populations.

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Appendix A

Branching Criterion for Generalized Logistic Equation

We begin by determining the critical point of the growth rate given by equation (4.6). Taking the first derivative with respect to y and evaluating at x and setting equal to 0,

$$\left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x} = \partial_y[\nu(y) - \rho(y)] - \partial_y[\alpha(y) + \beta(y)]K(x)C(x-y) - [\alpha(y) + \beta(y)]K(x)\partial_y C(x-y) \Big|_{y=x} = 0 \quad (\text{A.1})$$

Since the derivative is evaluated at $y = x$, we see immediately that $C(x-y) = 1$ and $\partial_y C(x-y) = 0$, while we can simply write ν , ρ , α and β as functions of x and take the partial with respect to x instead, leaving,

$$\partial_x[\nu(x) - \rho(x)] - K(x)\partial_x[\alpha(x) + \beta(x)] = 0 \quad (\text{A.2})$$

Solving this expression for $K(x)$ and setting it equal to the condition we found in equation (4.4)

$$K(x) = \frac{\partial_x[\nu(x) - \rho(x)]}{\partial_x[\alpha(x) + \beta(x)]} = \frac{\nu(x) - \rho(x)}{\alpha(x) + \beta(x)} \quad (\text{A.3})$$

Which gives us the condition,

$$\partial_x[\nu(x) - \rho(x)] \cdot [\alpha(x) + \beta(x)] - [\nu(x) - \rho(x)] \cdot \partial_x[\alpha(x) + \beta(x)] = 0 \quad (\text{A.4})$$

We then observe that since the derivative of K in equation (4.4) is

$$\partial_x K(x) = \frac{\partial_x[\nu(x) - \rho(x)] \cdot [\alpha(x) + \beta(x)] - [\nu(x) - \rho(x)] \cdot \partial_x[\alpha(x) + \beta(x)]}{[\alpha(x) + \beta(x)]^2} \quad (\text{A.5})$$

That equation (A.4) guarantees that $\partial_x K(x) = 0$. Using our expression for $K(x)$, (equation (4.5)),

$$\partial_x K(x) = \frac{(x-x^*)}{\sigma_k^2} e^{-(x-x^*)^2/2\sigma_k^2} \quad (\text{A.6})$$

We find that this gives us the condition that $y = x = x^*$ is indeed the critical point, as expected.

We now employ the machinery of Adaptive Dynamics by taking second derivatives of $s_y(x)$ to determine the nature of the critical point. For simplicity, we make the following assignments: $r(x) = \nu(x) - \rho(x)$ and $\phi(x) = \alpha(x) + \beta(x)$. For the same reason, we'll use primes to denote x derivatives and assume that r and ϕ are always functions of x without explicitly writing out the argument. We first take a look at the derivatives of K which will help us simplify our expressions. From equations (4.4) and (4.5) we have for the first derivative:

$$K' = \frac{r'}{\phi} - \frac{r\phi'}{\phi^2} = 0 \quad (\text{A.7})$$

and for the second derivative:

$$\partial_x^2 K(x) = -\frac{2r'\phi'}{\phi^2} + \frac{2r\phi'^2}{\phi^3} + \frac{r''}{\phi} - \frac{r\phi''}{\phi^2} = \frac{-K_0}{\sigma_k^2} \quad (\text{A.8})$$

Observe that multiplying both sides by $2\phi'/\phi$ we have:

$$\frac{2r'\phi'}{\phi^2} - \frac{2r\phi'^2}{\phi^3} = 0 \quad (\text{A.9})$$

Which lets us simplify our expression for the second derivative of K to:

$$\frac{r''}{\phi} - \frac{r\phi''}{\phi^2} = \frac{-K_0}{\sigma_k^2} \quad (\text{A.10})$$

We are now ready to consider the second derivative conditions. First, we look at the condition that x^* can invade, which requires the second x derivative to be positive:

$$\partial_x^2 s_x(y) \big|_{y=x=x^*} = \frac{2r'\phi'}{\phi} - r'' + \frac{r}{\sigma_c^2} - \frac{2r\phi'^2}{\phi^2} + \frac{r\phi''}{\phi} \big|_{x=x^*} \quad (\text{A.11})$$

Multiplying equation (A.9) by ϕ we realize that two of the terms cancel immediately, leaving two terms that are simply $-\phi \cdot K''$ (equation (A.10)). This lets us rewrite our condition as

$$\partial_x^2 s_x(y) \big|_{y=x=x^*} = \frac{K_0\phi}{\sigma_k^2} + \frac{r}{\sigma_c^2} \big|_{x=x^*} \quad (\text{A.12})$$

As long as $r > 0$ and $\phi > 0$, we have expression (A.12) which is always positive, satisfying our first condition. Our next condition is that x^* is invisable, which is satisfied if the following is positive:

$$\partial_y^2 s_x(y) \Big|_{y=x=x^*} = r'' - \frac{r\phi''}{\phi} + \frac{r}{\sigma_c^2} \Big|_{x=x^*} \quad (\text{A.13})$$

Recognizing two of the terms as being equal to $\phi K''$ (equation (A.10)) we can simplify our equation (A.13) for the x^* invasibility criterion to:

$$\frac{r}{\sigma_c^2} - \frac{K_0\phi}{\sigma_k^2} \Big|_{x=x^*} \quad (\text{A.14})$$

This equation is not trivially satisfied, but requires $r(x^*)\sigma_k^2 > K_0\phi(x^*)\sigma_c^2$. Dividing over the ϕ term, we have

$$\frac{r(x^*)}{\phi(x^*)}\sigma_k^2 > K_0\sigma_c^2 \quad (\text{A.15})$$

Recalling our first condition for K , equation (4.4) we see that $r(x^*)/\phi(x^*) = K(x^*) = K_0$, and we can simplify the condition for x^* to be invisable:

$$\boxed{\sigma_k > \sigma_c} \quad (\text{A.16})$$

Pressing on, the protected polymorphisms condition is:

$$[\partial_x^2 s_x(y) + \partial_y^2 s_x(y)]_{x=x^*} = \frac{2r'\phi'}{\phi} + \frac{2r}{\sigma_c^2} - \frac{2r\phi'^2}{\phi^2} \Big|_{x=x^*} \quad (\text{A.17})$$

From the condition imposed by $\phi \cdot K'$ this simplifies immediately to

$$[\partial_x^2 s_x(y) + \partial_y^2 s_x(y)]_{x=x^*} = \frac{2r}{\sigma_c^2} \Big|_{x=x^*} \quad (\text{A.18})$$

Which is clearly always positive as desired for branching. Finally, the condition for x^* to be an attractor (convergence stable) is:

$$[\partial_x^2 s_x(y) + \partial_y^2 s_x(y)]_{x=x^*} = \frac{2r'\phi'}{\phi} + \frac{2r\phi''}{\phi} - 2r'' - \frac{2r\phi'^2}{\phi^2} \Big|_{x=x^*} \quad (\text{A.19})$$

Canceling the same terms from the K' condition we're left with

$$= \frac{2r\phi''}{\phi} - 2r'' \Big|_{x=x^*} \quad (\text{A.20})$$

Which we recognize as $-\phi/2$ times K'' . Substituting gives

$$= \frac{2\phi K_0}{\sigma_k^2} \quad (\text{A.21})$$

Which again is positive, satisfying the convergence stability criterion. Hence our sole condition for this generalized logistic equation to have a branching point at x^* is $\sigma_k > \sigma_c$. If this is not satisfied, x^* still features protected polymorphisms, convergence stability, and can invade when rare, but can never then be invaded, hence it is an evolutionarily stable strategy.

Appendix B

Subsequent Branching

Here we use the particular form of the Logistic equation implemented in the simulation rather than the general form originally presented in the text. Our population will have the following dynamics:

$$S(y, x) = r - rK_x[C(x, y) + C(x, -y)]/K(y) \quad (\text{B.1})$$

We take the derivative with respect to y

$$\frac{\partial S(y, x)}{\partial y} \Big|_{y=x} = \frac{r[K_x C(-x, x) + K_x C(x, x)]K'(x)}{K(x)^2} - \frac{r[K_x \partial_y C(-x, y)|_{y=x} + K_x \partial_y C(x, y)|_{y=x}]}{K(x)} \quad (\text{B.2})$$

This simplifies under the following observations. We note that $K_x \equiv K(x)$, $C(x, x) = 1$, $\partial_y C(x, y)|_{y=x} = 0$, $\partial_y C(-x, y)|_{y=x} = (-2x/\sigma_c^2)C(-x, x)$, and $K'[x] = (-x/\sigma_k^2)K(x)$. Then we have

$$\frac{-x}{\sigma_k^2} r[C(-x, x) + 1] - r \left[\frac{-2x}{\sigma_c^2} C(-x, x) \right] \quad (\text{B.3})$$

Setting equal to zero we can immediately cancel r and x and solve for $C(-x, x)$:

$$C(-x, x) = \frac{\sigma_c^2}{2\sigma_k^2 - \sigma_c^2} \quad (\text{B.4})$$

We note that the left-hand side is greater than zero for $\sigma_k > \sigma_c$, the regime in which we are interested. Recall that since the form of C is fixed, this is a condition on the particular allowable values of x . Plugging in for $C(-x, x)$ we find the equilibrium point $x = a$ is given by

$$a = \pm \left[\frac{\sigma_c^2}{2} \log \left(\frac{2\sigma_k^2 - \sigma_c^2}{\sigma_c^2} \right) \right]^{\frac{1}{2}} \quad (\text{B.5})$$

Having found the stable points, we evaluate the second derivative of $S(y, x)$ with respect to y . If this is negative this equilibrium point $x = a$ is not invisable from rare mutants.

$$\begin{aligned} \frac{\partial^2 S(y, x)}{\partial y^2} \Big|_{y=x} &= \frac{1}{K(x)^2} [r[\\ &\quad C(-x, x)[-2K'(x)^2 + K(x)K''(x)] \\ &\quad + C(x, x)[-2K'(x)^2 + K(x)K''(x)] \\ &\quad - K(x) \cdot -2K'(x)[\partial_y C(-x, y)|_{y=x} + \partial_y C(x, y)|_{y=x}] \\ &\quad - K(x)^2[\partial_y^2 C(-x, y)|_{y=x} + \partial_y^2 C(x, y)|_{y=x}]] \quad (\text{B.6}) \end{aligned}$$

Taking the same conditions as before, and also the following conditions for second derivatives:

$$\begin{aligned} K''(x) &= \left(\frac{x^2}{\sigma_k^4} - \frac{1}{\sigma_k^2} \right) K(x) \\ \partial_y^2 C(x, y)|_{y=x} &= -1/\sigma_c^2 \\ \partial_y^2 C(-x, y)|_{y=x} &= \left(\frac{4x^2}{\sigma_c^4} - \frac{1}{\sigma_c^2} \right) C(-x, x) \end{aligned}$$

We then have:

$$\begin{aligned} \frac{\partial^2 S(y, x)}{\partial y^2} \Big|_{y=x} &= \frac{1}{K(x)^2} \left[r \left[\right. \right. \\ &\quad \left[C(-x, x) + 1 \right] \left[-2 \left(\frac{-x}{\sigma_k^2} \right)^2 K(x)^2 + \left(\frac{x^2}{\sigma_k^4} - \frac{1}{\sigma_k^2} \right) K(x)^2 \right] \\ &\quad + 2 \left(\frac{-x}{\sigma_k^2} \right) K(x)^2 \left(\frac{-2x}{\sigma_c^2} \right) C(-x, x) \\ &\quad \left. \left. - K(x)^2 \left(\frac{4x^2}{\sigma_c^4} - \frac{1}{\sigma_c^2} \right) C(-x, x) - K(x)^2 \left(\frac{-1}{\sigma_c^2} \right) \right] \right] \quad (\text{B.7}) \end{aligned}$$

Simplifying, we have

$$\begin{aligned} &= rC(-x, x) \left[-2 \frac{x^2}{\sigma_k^4} + \frac{x^2}{\sigma_k^4} - \frac{1}{\sigma_k^2} + \frac{4x^2}{\sigma_k^2 \sigma_c^2} - \frac{4x^2}{\sigma_c^4} + \frac{1}{\sigma_c^2} \right] \\ &\quad + r \left[-2 \frac{x^2}{\sigma_k^4} + \frac{x^2}{\sigma_k^4} - \frac{1}{\sigma_k^2} + \frac{1}{\sigma_c^2} \right] \quad (\text{B.8}) \end{aligned}$$

Recalling our condition for $C(-x, x)$ in equation (B.4) and simplifying we can rewrite this as:

$$\frac{-2\sigma_k^4 + 4\sigma_k^2 x^2 + 2\sigma_c^2(\sigma_k^2 - x^2)}{\sigma_c^2 \sigma_k^2 (\sigma_c^2 - 2\sigma_k^2)} \quad (\text{B.9})$$

Since the denominator is negative for $\sigma_k > \sigma_c$, we need the numerator to be positive for the point a to be stable. Using our solution for $x = a$ given in equation (B.5), we find that this amounts to the condition:

$$\left(2\frac{\sigma_k^2}{\sigma_c^2} - 1\right) \log \left(2\frac{\sigma_k^2}{\sigma_c^2} - 1\right) + 2 \left(\frac{\sigma_k^2}{\sigma_c^2} - \frac{\sigma_k^4}{\sigma_c^4}\right) \quad (\text{B.10})$$

This term is always negative for $\sigma_k > \sigma_c$, hence this point is always unstable. It is a straight forward exercise to show that the other conditions are always satisfied.

Appendix C

Simulation Code

Simulations were carried out in MATLAB®7.1.

```

clear %Clear existing variables
start = clock; %initialize a timer for code runtime
MaxEvents = 100000000; %Number of events (iterations) Go ahead, max out MATLAB's
variable size
MaxVariants = 10000;

%Variable assignments,
K_0 = 500; % Carrying capacity at x_0
x_0 = 0; % Optimal trait value
sigma_k = 1; % sd of carrying capacity
sigma_c = .4; % sd of competition weighting
r = 1; % birthrate
mu = .001; %Mutation rate
sigma_mu = 1/20; %standard deviation for mutant traits

cut = 100; %Don't plot populations of size less than this
Plots = 100; %number of times to plot
F = 1; %Figure number to use

disp(['MaxEvents= ', num2str(MaxEvents), ', MaxVariants = ', num2str(MaxVariants),
', \mu = ', num2str(mu), ', \sigma_k = ', num2str(sigma_k), ', \sigma_c = ',
num2str(sigma_c), ', \sigma_{\mu}= ', num2str(sigma_mu)])

%Function definitions, matching D&D99
K = @(x) K_0*exp(-(x-x_0).^2/(2*sigma_k^2));
C = @(x,y) exp(-(x-y).^2/(2*sigma_c^2));

% Initialize variables:
pop = zeros(2,MaxVariants); %Population matrix: Row 1 = trait values, Row 2 = pop
size
Kvector = zeros(1, 200);
Cmatrix = zeros(200, 200);
N = zeros(1,MaxVariants);
sep_history = zeros(1, 100);
history = zeros(2, 100, Plots);
PlotInterval = round(MaxEvents/Plots);

%Stable distribution of dimorphism
a = sqrt(sigma_c^2*log( (2*sigma_k^2-sigma_c^2)/sigma_c^2) / 2);
disp(['Predicted equilibrium dimorphism = +/- ', num2str(a)])

%Initial Population Conditions:
variants = 1; %Number of different trait values in population
pop(1,1:variants) = [x_0]; %starting trait value(s)
pop(2,1:variants) = [K_0]; %starting population of those traits

%Calculate initial Kvector and Cmatrix from initial conditions
Kvector(1:variants) = K( pop(1,1:variants) );
for i = 1:variants
    Cmatrix(i,1:variants) = C( pop(1,i), pop(1,1:variants) );
end

```

```

Cmatrix = sparse(Cmatrix);
time = zeros(1,MaxEvents); %intitalize time

%Define a function for death based on D&D99
deaths = @(x, pop) (r*(pop(2,:)*C(x,pop(1,:))')./K(x));

%prints the initial setup
disp(['initial traits = ', num2str(pop(1,1:variants)), ' with pops of ',
num2str(pop(2,1:variants))])

fig = 0; %figure numbering for during run
sep = 0; %seperation history counter
j = 0; %mean trait counter
figure(F); clf; hold on; %overlay plotting of trajectory

for t=1:MaxEvents
    N = pop(2,1:variants); %Populations of those traits
    death = N.*(r*( Cmatrix(1:variants, 1:variants)*N' )
./Kvector(1:variants)')); % mean deaths, d*N
    birth = r.*N; % mean births, r*N
    overallRate = sum(birth)+sum(death); %Events weighted as fraction of
overall rate
    tmpy = cumsum([birth, death])/overallRate;
    tmpx = rand;
    event = find(tmpx < tmpy & tmpx >[0 tmpy(1:end-1)]);
    time(t) = log(1/rand)/overallRate; %Time at which event occurred
    if event <= variants %If event is a birth...
        if rand < mu
            variants = variants + 1; %New variant (assume no mutation
to existing phenotype)
            if variants >= MaxVariants
                disp('Variants exceed Maximum Variants');
                break;
            end
            trait = pop(1,event); % Trait value of pop with birth,
needed for mutant calc
            pop(1, variants) = normrnd(trait, sigma_mu); % determine
mutant trait value
            pop(2, variants) = 1; % Make one individual with the new
trait
            Kvector(variants) = K(pop(1,variants) ); %Carrying
capacity of new trait

            alive = find(pop(2,:)); %index values of the nonzero
population traits
            pop = pop(:,alive); %Clean up pop!
            Kvector = Kvector(alive); %tracks only living traits!
            variants = length(alive);
            Cmatrix = zeros(200,200);%Rewrite the entire Cmatrix!
            for i = 1:variants
                Cmatrix(i,1:variants) = C( pop(1,i),
pop(1,1:variants) );
            end

```

file:///home/cboettig/Documents/springjp/codePage2.m

```

else
    pop(2, event) = pop(2, event)+1; % no mutant? increase pop
by 1
end

end
if event > variants %If event is death, decrease that pop by 1
    pop(2, event-variants) = pop(2,event-variants)-1;
end

%Optional reporting pieces of code, not integral to simulation:
if rem(t-1,PlotInterval) == 0 %Plot as we go
    fig = fig+1;
    %figure(fig); clf;
    living = pop(:, pop(2,:) > cut );
    types = size(living,2);
    T = sum(time);
    %S = max(round(living(2,:)), 2); %Use this for K_0 = 50 instead of
500
    S = max(round(living(2,:))*(100/K_0), 4);
    pause(.1)
    for l = 1:types
        plot(T, living(1,l), 'k.', 'MarkerSize', S(l))
    end

    %Display basic information
    fprintf('\n');
    disp(['total population = ', num2str(sum(living(2,:))), ', ',
Simulated Time = ', num2str(sum(time)), ', variants = ', num2str(variants), ', ',
num2str(round(100*t/MaxEvents)), '% done'])%display populated traits
    % fprintf('Running Time = %.0f sec\n', etime(clock, start))% Display
running time

    %Keep a record of plotted data
    history(1:2, 1:size(living,2), fig) = living;
    cumtime(fig) = sum(time);
end
if rem(t, MaxEvents/1000) == 0
    fprintf('=')% prints primitive percent done bar
    %Record mean trait level for D&L comparison, uses 1000 sample
points
    j = j+1;
    mean_x(j) = pop(1,:)*pop(2,:)/sum(pop(2,:));
    t_value(j) = sum(time);
    plot(t_value, mean_x)
end
end
fprintf('\n');

%Title the graph
title(['\mu = ', num2str(mu), ', \sigma_k = ', num2str(sigma_k), ', \sigma_c = ',
num2str(sigma_c), ', \sigma_{\mu} = ', num2str(sigma_mu), ', T = ',
num2str(sum(time)), ', variants = ', num2str(variants) ])

```

file:///home/cboettig/Documents/springjp/codePage3.m

```
%gillespie10.m, by Carl Boettiger
%Created 042006, edited 042606
```

```
plot(t_value, mean_x);%plots mean trait trajectory
```

```
%Display title info to screen
```

```
disp(['\mu = ', num2str(mu), ', \sigma_k = ', num2str(sigma_k), ', \sigma_c = ',
num2str(sigma_c), ', \sigma_{\mu} = ', num2str(sigma_mu), ', T = ',
num2str(sum(time)), ', variants = ', num2str(variants) ])
```

```
%display other info
```

```
disp(['total population = ', num2str(sum(living(2,:))), ', Simulated Time = ',
num2str(sum(time)), ', variants = ', num2str(variants)])%display populated traits
```

```
fprintf('Running Time = %.0f sec\n', etime(clock, start))% Display running time
```

```
%*****CHANGELOG*****
```

```
%The Gillespie Algorithm for and Dieckmann and Doebelli style
```

```
%Logistic asexual population.
```

```
%v2 Keeps track of time and includes mutations (new to v2). Plots population of
each trait as it runs.
```

```
%v3: probabilities done the smart way.
```

```
%v4: probabilities done the smart way CORRECTLY!
```

```
%v5: plots of predicted final distribution, etc
```

```
%v6: Lookup method for K and C: Doesn't compute K and C
```

```
%more v6: much more info read out and modification
```

```
%v7: More frequent readout, stores sepeartion history
```

```
% each time but stores K in a vector and C in a matrix
```

```
%v8: Plots populations (above cutoff level) against time
```

```
% as the code runs. Dot size indicates population level
```

```
%v9: Can calculate weighted average trait as a function of time for the run
```

```
% Comment out necessary lines when not wanting this feature to save time!
```

```
%v10: Clever use of lookup keeps vectors small made everything uberfast! Limiting
step is MATLABs looking up random number speed
```