**Transient evolutionary attractors alter evolutionary adaptation**

John P. DeLong and Clayton E. Cressler

University of Nebraska – Lincoln, Lincoln, NE, 68588, USA

**Abstract**

Adaptation requires alignment of population traits with traits that maximize fitness given the environmental conditions. The path toward adaptation, however, is subject to dynamic ecological forces that can alter evolutionary outcomes. How these ecological forces alter the path and pace of evolution, however, are not well understood because the backbone of evolutionary theory typically rests on the assumption of ecological equilibrium or a separation of evolutionary and ecological time scales. Here we relax these assumptions and evaluate patterns of adaptation in a population growing with simple logistic type dynamics. We show that when populations are not at equilibrium that they may show transient evolutionary attractors that alter the path of evolution. We also compare the eco-evolutionary trajectories generated by Gillespie eco-evolutionary models with the expectations of the same system from quantitative genetics and adaptive dynamics and find that 1) transient dynamics can drive evolution toward transient evolutionary attractors that compete with the overall evolutionary stable strategy, and 2) stochasticity both reduces genetic variation, reducing the pace of evolution, and shifts populations toward the transient optima. We further show that harvesting that maintains populations in transient states can redirect evolution away from an ESS and toward optima that are not identified using equilibrium techniques. Our results clarify that considering the path toward adaptation during transient periods can greatly improve our understanding of the path and pace of evolution.

**Introduction**

Adaptation occurs as populations follow paths through trait space toward a good match between traits in a population and the traits that maximize fitness given the environmental context. The context can be visualized using a fitness landscape where peaks represent locally optimal trait values (Wright 1931), and a population can be said to be adapted when its traits align with the peak. Such optima represent trait combinations that maximize fitness, defined approximately as lifetime reproductive success. Populations can evolve up-slope toward these fitness peaks, barring hindrances such as the lack of genetic variation. Classical approaches to identifying fitness peaks typically start by assuming an ecological equilibrium and asking what trait(s) maximize fitness at this equilibrium (Lande 1976, 1982; Abrams et al. 1993*a*). This approach is fundamental to a wide array of theoretical work aimed at understanding the process of adaptation (bunch of cites) (Fussmann et al. 2003; Cortez and Ellner 2010; Vasseur et al. 2011; Cortez 2016).

It is increasingly recognized, however, that eco-evolutionary feedbacks may alter the effect of specific traits on the components of fitness, altering the fitness landscape and the location of adaptive peaks (Govaert et al. 2019). These feedbacks can be quite rapid, since the timescales of ecology and evolution are not as different as sometimes thought (Hairston, Jr. et al. 2005; Schoener 2011; DeLong et al. 2016). For example, selection may fluctuate between favoring grazing resistant and rapidly growing forms of algae due to cycles of grazing activity by rotifers (Yoshida et al. 2004). Such fluctuations require that the relationship between traits and fitness are changing rapidly through time, such that a population evolves in one direction and then another as the context changes.

Although fitness landscapes may change dynamically through such eco-evolutionary feedbacks, additional processes may influence the fitness landscapes and the ability of populations to climb toward fitness peaks. Here we consider two such processes: transient dynamics and stochasticity. First, an overlooked feature of shifting fitness landscapes is that even in a model without eco-evolutionary feedbacks, density dependence in either births or deaths implies that the effect of a trait on fitness differs between equilibrium and transient states. If populations experience different selective forces in transient phases than at equilibrium, then the path and pace of evolution might be quite different between transient and equilibrium phases. Second, stochasticity can alter both the ecological dynamics and the direction and speed of evolution. For example, demographic stochasticity can lead to genetic drift, causing maladaptation through the random loss of optimal genotypes or by generating wandering paths of trait change (Crespi 2000; Lenormand et al. 2009). Given that most populations experience stochasticity and do not typically reside at an ecological equilibrium, it is crucial to consider how our expectations for evolution could be altered by transient dynamics and stochasticity.

To understand how transient dynamics and stochasticity might influence the path and pace of adaptation, we undertake a theoretical exploration in two parts. In part one, we introduce a simple population model and describe evolutionary predictions based on deterministic approaches that invoke ecological equilibria or a separation of ecological and evolutionary timescales (i.e., quantitative genetics (QG) and adaptive dynamics (AD)). We also show that when a population described by such a model is not at equilibrium there are transient evolutionary attractors (TEAs) that influence the evolutionary dynamics. In part two, we implement this population model as a Gillespie eco-evolutionary model (GEM) to determine whether evolution responds to these TEAs rather than the equilibria identified using QG/AD approaches. We foster transient conditions in two ways: 1) by varying the location of the ecological equilibrium (i.e., carrying capacity), allowing stochasticity to influence population growth to different degrees, and 2) by introducing a cull to maintain populations below their equilibrium. Together, our results indicate that TEAs may arise whenever density dependence influences birth or death rates and that these TEAs may play an important role driving evolutionary dynamics. We suggest that understanding transient evolutionary phenomenon may provide new insights into how managed populations evolve and an alternative explanation for evolutionary patterns that seem maladaptive.

**Part One: Transient versus equilibrium evolutionary expectations**

Lande (1976, 1982) derived an expression for the dynamics of trait change from classical quantitative genetics (Falconer 1960), showing that the average trait in a population changes at a rate that is proportional to both genetic covariance and the gradient of fitness with respect to the trait. Work by Peter Abrams and colleagues (Abrams et al. 1993*a*, 1993*b*; Abrams and Matsuda 1997) integrated Lande’s model of trait change with models of ecological dynamics by assuming that fitness could be represented by the per-capita growth rate of the evolving population. These QG models are eco-evolutionary models, with the relative timescales of ecological and evolutionary dynamics given by the genetic (co)variance.

The adaptive dynamics approach (Geritz et al. 1998) often leads to identical evolutionary predictions (Abrams et al. 1993*a*), but arrives there through a different analysis. Trait evolution, in adaptive dynamics, happens by a process of mutation and invasion. Specifically, the analysis asks whether a monomorphic population could be invaded by a mutant population with a different trait value (determined by the dominant eigenvalue [or Lyapunov exponent] of the system evaluated at the mutant-free attractor; Metz et al. 1992; Geritz et al. 1998). The direction of trait evolution is given by the derivative of this “invasion fitness” with respect to the trait.

Another shared feature of the QG and AD approaches is that changes in ecological variables are typically assumed to be much faster than changes in trait dynamics. The AD approach assumes a strict separation of timescales, whereas the QG approach typically assumes that the genetic covariance term is small, slowing evolution relative to ecology (although there has been recent work relaxing this assumption and showing it can have non-intuitive effects on both ecological and evolutionary dynamics; Cortez and Ellner 2010; Cortez and Weitz 2014; Cortez 2016). The consequence of this assumption is that the dynamics of the system tend to be determined much more by the dynamics of the “fast” subsystem (Cortez and Ellner 2010). In an eco-evolutionary context, that means that the system will move quickly to an ecological equilibrium that will change slowly as the mean trait changes. Under this view, then, the transient behavior of the ecological system has very little effect on the path towards adaptation.

For example, consider this simple modified logistic model of population growth (Appendix S1). The model is:

Equation 1.

where *R* is population abundance, *t* is time, *b*max is maximum birth rate (i.e., fecundity), *d*min is minimum death rate, and *b*s and *d*s characterize the effect of population abundance on the realized birth and death rates, respectively. We consider the case where *b*max (i.e., fecundity) is evolving and connected to mortality through a trade-off described by an accelerating function:

, Equation 2

where *s* is the value of *d*min when *b*max = 1. Using the QG approach (Lande 1976; Abrams et al. 1993*a*), the dynamics of the population mean are proportional to heritable trait variation (the product of heritability *h*2 and the amount of additive genetic variation *V*) and the gradient of the per-capita growth rate with respect to , evaluated at the mean: (Appendix S1), giving

Equation 3

In this model, the mean trait will evolve toward the evolutionary equilibrium . It is straightforward to show that this equilibrium is an evolutionarily stable strategy (ESS) that maximizes fitness.

Alternatively, we can use expected lifetime reproductive success (LRS) as a measure of fitness, which is the product of the expected birth rate given and lifespan (1/death rate). In this model, this is

Following Lande’s derivation, the dynamics of the population mean would be given by

Equation 4

At the ecological equilibrium , the equation for the trait dynamics becomes

where . Although this expression is more complicated than the one in Eq. (3), it has the same evolutionary equilibrium: (Appendix S2).

However, if the system is away from the ecological equilibrium, the evolutionary equilibrium is:

Equation 5

Equation 5 suggests that when the system is undergoing transient ecological dynamics, the trait may actually evolve towards a different evolutionary equilibrium than the one that is predicted by a QG/AD approach. Since this equilibrium always depends on population size, any force (such as stochasticity, harvesting, or individual trait variation) acting on the population to slow down its ecological approach to equilibrium would cause evolution to proceed towards equilibria that are not the ESS. We refer to these equilibria as transient evolutionary attractors (TEAs). These TEAs are critical to understanding how transient dynamics and external impacts can redirect populations toward trait values that would be viewed as maladaptive values given a QG/ESS framework. We emphasize that any model in which the evolving component of LRS is a function of population size will have a derivative that includes population size, generating a difference between transient and equilibrium conditions.

**Part Two: Transient evolutionary trajectories revealed by GEMs**

**Methods**

*About GEMs*.—GEMs simulate the dynamics of an ODE model by breaking down rates of change for the population as a whole into discrete birth and death events (DeLong and Gibert 2016; DeLong and Luhring 2018; DeLong and Belmaker 2019). GEMs build on the standard Gillespie algorithm that simulates ODE models where demographic stochasticity (random variation in the sequence and number of demographic events) influences the outcomes (Gillespie 1977; Yaari et al. 2012). GEMs also incorporate demographic heterogeneity (variation among individuals in demographic traits) by giving every individual a trait value drawn from a distribution with known mean and variance. Thus, a standard Gillespie might represent a population size by a number, such as 10, whereas a GEM represents this population with a vector of 10 traits. In a GEM, an individual’s trait value determines its probability of giving birth or dying.

GEMs function in an iterative cycle of birth and death events. Rather than taking a constant parameter value, as in a standard Gillespie simulation, the random draw of a trait from the trait vector is used either as a parameter or as a trait that influences a parameter. Thus, each individual experiences a particular probability of birth or death depending on their traits. Once the individual is chosen and the rate terms are calculated, an event is randomly chosen ‘wheel-of-fortune’ style. If the event is a death, that individual (and its trait) are removed from the population. If the event is a birth, a new individual is added to the population given some rule for heritability of that trait. In these simulations, we follow the heritability rules set out in (DeLong and Luhring 2018; DeLong and Belmaker 2019) with the change that we are not using here the weighted mean for the parental trait. Thus, an offspring trait is randomly drawn from a lognormal distribution with a mean of , where *b*max is the actual trait of the current parent and is the current population mean. The standard deviation of this distribution is given as , where *b*init is the distribution of *b*max in the initial population. As a GEM is running, the loss and addition of individuals in the population affects both population dynamics and the dynamics of both the mean and variance of the trait distribution. Populations gradually lose individuals with high likely of mortality and gradually add individuals with higher likelihood of births, generating natural selection without needing to specify explicit equations for the trait dynamics or without needing to identify explicitly the expected trait equilibria such as an ESS.

The inclusion of both demographic heterogeneity and stochasticity increases the realism of GEM outcomes. This is because in real populations, variation in fitness arises from two components. First, real demographic heterogeneity allows populations to distribute along some curve that links traits to fitness (Figure 1A). If that curve is unimodal, a fitness peak occurs at the top of the curve. By including a distribution of individuals that vary in expected fitness, GEMs allow demographic heterogeneity to influence ecological and evolutionary outcomes (Kendall et al. 2011; Stover et al. 2012; Cressler et al. 2017). Second, individual demographic stochasticity causes individuals to randomly deviate from the expectation given by the fitness-trait curve (Figure 1A). Even with an optimal trait, individuals may randomly display high or low fitness through chance alone (van Daalen and Caswell 2017). For example, Banks and Thompson (1987) assessed lifetime reproductive success of the damselfly *Coenagrion puella* with respect to individual head width (Figure 1B). Although there was a clear fitness-maximizing value of head width, the realized lifetime reproductive success of individuals was quite variable, and many individuals with the optimal head width realized relatively low fitness (Figure 1B).

On top of individual variation in realized fitness, population-level demographic stochasticity (random variation in the sequence and number of demographic events) has long been recognized to have important effects on the dynamics of adaptation, for example through genetic drift (Lenormand et al. 2009) or the loss of high-fitness genotypes (Crespi 2000). Note that a key difference between the QG approach, in which the trait variance is constant, and GEMs is that genetic drift is an inherent possibility in GEM simulations, depending on population size and the degree of stochasticity.

*Sets of comparisons*.—We ran three sets of simulations, each with a specific purpose:

Comparison 1: We first examined the role of individual variation in *b*max on the ecological dynamics of this model when no evolution was possible. To do this, we set heritability *h*2 = 0 and introduced variation in traits in the population with CV = 0.3. Because in our model, the *d*min is locked to *b*max, we examined whether variation in neither trait, *b*max alone, *d*min alone, or both traits combined, influenced the dynamics. This examination also confirmed whether in the absence of trait variance that the GEM dynamics reduced to a standard Gillespie simulation of the model dynamics.

Comparison 2: We next evaluated differences between the GEM, QG, and adaptive dynamics approaches by comparing outcomes across different values of *b*s and *d*s, which set the strength of density dependence on birth rates and death rates, respectively (Equation 1). Varying these two parameters effectively changes the carrying capacity of the system such that starting at any given population size means starting at a different distance from equilibrium. These parameters also influence the effect of population abundance on the TEAs (Equation 5), altering the location of the attractors across scenarios. We expected that these simulations would vary in the amount of stochastic loss of trait variation because of the different rates populations would grow at the start of the simulation. We initiated these populations at a population abundance of five and allowed them to grow.

Comparison 3: Finally, we asked whether harvesting of a population that has already achieved an ESS trait and ecological equilibrium would cause it to evolve toward a TEA as long as the perturbation persisted. We do this with the lightest level of density dependence with three levels of culling and predicted that populations in each scenario would move to the TEA for the culled population size. We also predicted that stochastic loss of genetic variation could slow approach toward the TEA.

*Modeling details*.—In all simulations except with an ESS starting point, we started the populations with *b*max = 1.8, *d*min = 0.3, and thus s = 0.0926. The ESS *b*max for this system is 5.4, which means the ESS *d*min is 2.7. We make density dependence in births and deaths symmetrical, so *b*s = *d*s, and set these equal to 0.1, 0.01, and 0.001 to generate a gradient in density dependence. With these values, the equilibrium abundance (*K*) across scenarios at the start of the simulation is 7.5, 15, and 75, and at the ESS (since the equilibrium is a function of the parameters) it is 13.5, 135, and 1,350. We initialize populations at five individuals in the first two comparisons but start simulations at the equilibrium trait and abundance in the third, culling comparison. We ran each simulation for 60 time steps, which was long enough to reach the ecological equilibrium in all non-evolutionary scenarios, and for 50 replicate simulations. Unless otherwise indicated, the variation in *b*max was set with a CV = 0.3 and the heritability was set at 0.75.

To evaluate patterns in individual fitness across GEM simulations, we tracked the number of reproduction events and the lifespan for each individual. This allowed us to show the realized relationship between the trait *b*max and lifetime reproductive success, akin to Figure 1B. We do this for the initial population (born before time step 1) and the population toward the end of the simulation (born after time step 50). For the latter, we only included individuals that died before the end of the simulation. We use these data to illustrate how the distribution of traits line up with either the ESS or the TEA traits across our different simulations.

**Results**

Comparison 1: Reducing heritability to zero, effectively eliminating evolution by natural selection, revealed that trait variation *per se* altered the dynamics of the system (Figure S1). Variation in *b*max alone reduced the equilibrium abundance of the population. Variation in *d*min alone had little effect on the population, but combined with *b*max, *d*min reduced the equilibrium abundance of the population even more (by about 7% below the expected equilibrium). This result indicates that variation *per se* is one factor that may limit the populations in our simulations from achieving the expected equilibria.

Comparison 2: In our first set of simulations, in which we varied only the strength of density dependence, we found that all populations grew and evolved *b*max in the direction of the ESS (Figure 2, 2nd and 4th rows). Although no population was able to grow or evolve as fast as expected from QG (Figure 2, 1st and 2nd rows), the population experiencing the least density dependence was on track for the mean population trait () to reach the ESS trait value and population equilibrium at the end of the 60 days.

We also found that populations with steeper density dependence slopes (i.e., lower *K*) experienced greater initial loss of trait variation (Figure 2, 3rd row), slowing the pace of evolution relative to that expected by quantitative genetics. Variation also remained near the initial level for longer when density dependence was weaker (Figure 2, second row). At intermediate and low density dependence, the initial loss of trait variation was regained, allowing populations to recover from the effects of low-density stochasticity and continue moving in the direction of the ESS. The effects of stochasticity were noticeably higher for small populations, with considerably more variation in abundances through time for populations with the highest density dependence (Figure 2, left column). All populations displayed considerable individual demographic stochasticity (Figure 2, bottom row), with individual variation in lifetime reproductive success peaking at or near the ESS but with massive individual differences even among individuals with the same traits.

The fitness landscapes governing adaptation in these systems varied as populations grew, generating TEAs that shifted along with the population (Figure 3). Populations moved along these fitness contours as the population grew toward its ecological equilibrium. Population trajectories, however, showed considerable variation when density dependence was strong, preventing approach to either the local TEA or the ESS, while populations with low density dependence displayed a smooth, direct approach toward the ESS.

Comparison 3: In our third set of simulations, we applied a persistent cull to populations that had already achieved their ESS trait and abundance values. Evolution in these scenarios generated clear movement of the populations toward the population-specific TEAs that varied with the magnitude of the cull (Figures 4,5). Rather than returning to the ESS, populations that were reduced to a lower abundance shifted their path immediately to head upslope toward the abundance-determined TEA and not toward the ESS (Figure 5). The populations followed a path of adaptation specific to a transient dynamics state, as generated by Equation 5, not the path generated by equilibrium conditions.

**Discussion**

Evolutionary theory today encompasses a wide range of modeling techniques and frameworks that facilitate an understanding of how populations evolve and adapt to their environments (Lande 1982; Abrams et al. 1993*a*; DeAngelis and Mooij 2005; Coulson et al. 2006; Ellner and Rees 2006; Lion 2017; de Vries and Caswell 2019; Govaert et al. 2019). From eco-evolutionary quantitative genetics models to individual-based models, integral projection models, matrix models, and population genetics, it is increasingly clear that evolution can be surprising and yet logical at the same time. Our analytical results and those using GEMs contribute to this dichotomy by demonstrating that populations not at equilibrium may evolve toward temporary attractors and not a global ESS whenever components of fitness (birth and death rates) are density dependent. The eco-evolutionary dynamics and the pace and path of evolution, then, are qualitatively and quantitatively different from predictions that overlook transient periods of evolution. The transient evolutionary dynamics that unfolded during our GEM simulations here responded to underlying fitness contours that are invisible with an equilibrium lens but that lay out a straightforward evolutionary path that transient populations can follow. With the rapid environmental change and direct human impact on populations occurring throughout the world today, we anticipate that transient theories of evolution will provide crucial new insights into the adaptation of wild populations.

In addition to the effects caused by the transient fitness landscapes, our results indicate substantial challenges to our expectations of evolution arising from QG/AD approaches. The presence of individual trait variation (and demographic heterogeneity), although required for evolution to proceed, can change the ecological dynamics. In our case, by suppressing population sizes, this variation simultaneously facilitated evolution and maintained the system in a transient state, limiting evolution. Individual demographic stochasticity, abundantly displayed in our results, clearly stripped individuals of their expected fitness benefits while allowing individuals with low fitness traits to have high fitness. This effect should result in a flattened fitness gradient relative to the expectations from quantitative genetics, greatly reducing the rate of evolution. Finally, population-level stochasticity, the aggregate change in sequence of events, generated heightened variation in population size for small populations, both keeping populations in transient states and leading to substantial loss of genetic variation. Examination of the population dynamics in the systems with lower carrying capacities (Figure 2) indicate substantially more variation in population sizes, reflecting high stochasticity. All together, these forces substantially slowed evolution relative to expectations generated from assumptions of large population size, equilibrium conditions (fast ecology), and deterministic trait-fitness benefits.

Increasing evidence indicates that ecological dynamics can play a crucial role in driving evolution. Furthermore, evolution within systems not at equilibrium, and rather displaying transient dynamics, can alter the ecological dynamics and therefore reset the selective forces acting on the population (Fussmann et al. 2003; Yoshida et al. 2003; Cortez and Weitz 2014). Our results further this finding, demonstrating that even simple, single-species models can facilitate not just eco-evolutionary dynamics but transient attractors that may compete with the overall evolutionary attractor in the system. By relaxing the assumption of fast ecology/slow evolution or equilibrium conditions, and taking into account the full consequences of individual variation and stochasticity, we may generate more realistic predictions for evolution.

Our results also have clear implications for managed populations. Economically important populations, from fisheries to ungulates and invasive species, may show substantial changes in traits in response to random or trait-biased harvesting (Darimont et al. 2009). In Windermere pike (*Esox lucius*), for example, harvesting is thought to have altered the fitness landscape and generated selection away from the direction driven by the natural setting (Edeline et al. 2007). This effect could represent both the direct selective effects of harvesting itself but also the presence of a transient attractor that competed with an ESS attractor, since harvesting maintained populations in a transient state. Understanding evolution in such populations may require a disequilibrium (transient) approach, because harvested populations are by definition being held below their potential equilibrium. To the degree that these populations show density dependence in their birth or death rates, similar to but not necessarily following the birth-death logistic model, they are likely to also display TEAs that could draw their traits away from the starting values, whether the initial trait distributions are at the ESS value or not. Harvesting our simulated population at something near the maximum sustainable yield, for example, could nearly halve the fecundity of the population, even without harvesting having a direct selective effect. In the birth-death logistic model, the ecological equilibrium depends on these traits, and so evolution toward the TEA would further alter the system and potentially lead to unexpected shifts in both traits and abundance.

In conclusion, our results indicate that individual variation and stochasticity represent severe hindrances to evolution, at least with respect to the expectations from deterministic fitness outcomes, equilibrium conditions, and a separation of ecological and evolutionary timescales. Furthermore, focusing on evolution in transient states revealed powerful competing evolutionary attractors (TEAs) that have not factored into much (if any) current thinking on the pace and path of adaptation. Becoming aware that evolution is relatively fast, and that many populations are in transient states rather than equilibrium states, may be essential for a fuller understanding of adaptation.

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Figure 1. Variation in the relationship between traits and fitness. **A**. A depiction of how stochasticity and heterogeneity map on to the relationship between traits and fitness. **B**. An example of this relationship with the damselfly *Coenagrion puella* (Banks and Thompson 1987). These data show that lifetime reproductive success (here lifetime clutches) may reach a peak at some intermediate trait value. Simultaneously, individuals may vary dramatically in their realized fitness despite an expected fitness outcome.

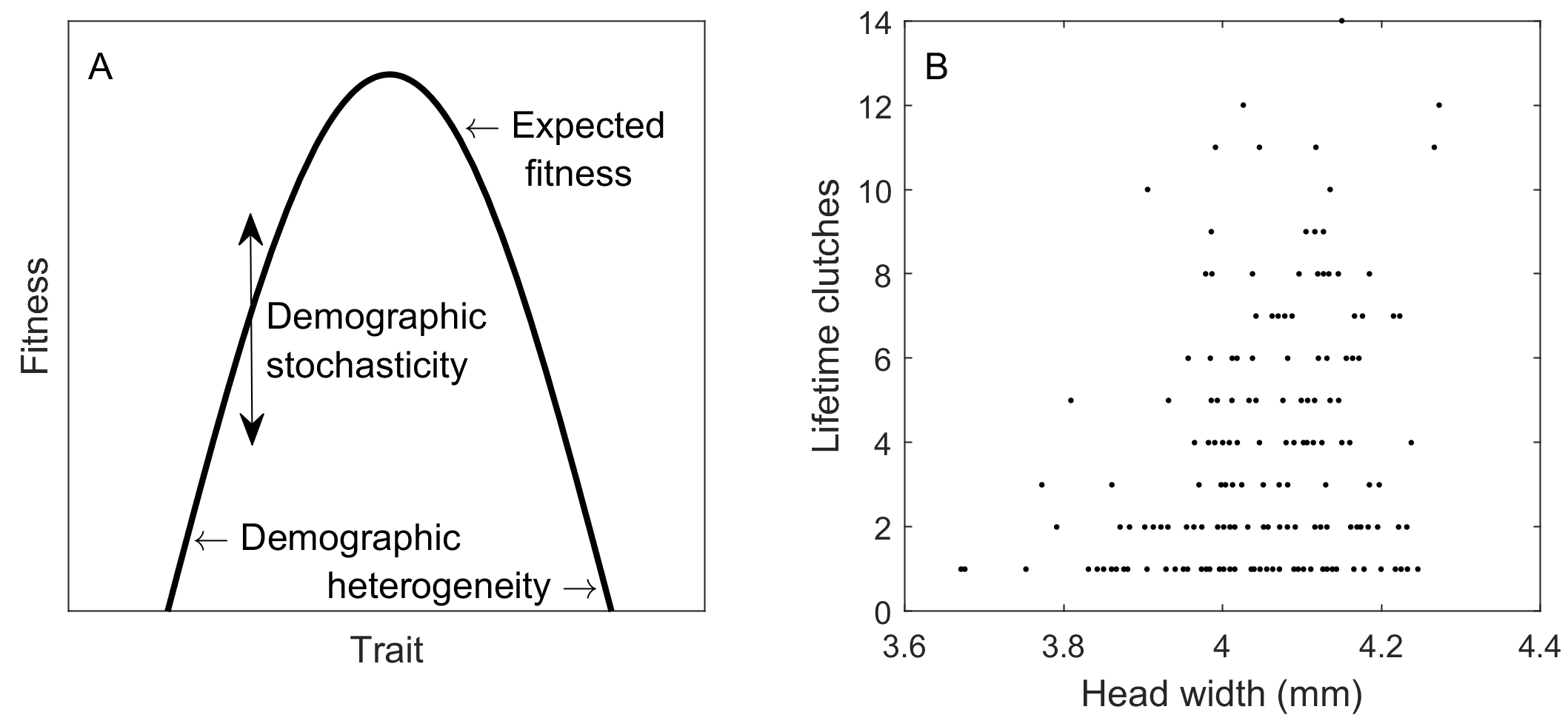


Figure 2. Results of Gillespie eco-evolutionary model (GEM) simulations of the birth-death logistic model. The rows show from top to bottom population abundance (y axis limits vary), mean *b*max, and variance in *b*max. The columns show three levels of density dependence in birth and death rates (values of *b*s and *d*s), decreasing in strength from left to right. The GEM simulations and middle 50% of observations are in purple and light purple, respectively. The quantitative genetics (QG) solution is in bold orange and the evolutionary stable strategy (ESS) is shown with a dashed orange line in the top two rows and a solid vertical line in the bottom row. The initial traits and equilibrium abundances are shown with dashed black lines, and the transient evolutionary attractors (TEAs) are in pink (dashed in row two and solid vertical in row four). Lifetime reproductive success at the beginning (gray dots) and at the end of the simulation (black dots) as a function of *b*max include only individuals that completed their lives.

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Figure 3. Fitness landscapes of the systems represented in Figure 2. Variation in the fitness landscape caused by changes in abundance are shown with the sequences of black dots, such tha the landscapes tend to get flatter toward the ESS and the ecological equilibrium. The gray line connects the transient evolutionary attractors (TEAs) across density levels. The simulations were initiated at the abundance and trait values indicated by the red dot, with the populations proceeding along the orange line. The evolutionary stable strategy (ESS) of the system is shown by the blue dot, and the competing TEA at the population size occurring by the end of the simulation is shown in teal. From left to right, the panels show the trajectories from Figure 2, with decreasing density dependence and thus a higher carrying capacity toward the right. When density dependence is high, and populations remain relatively small, substantial stochasticity limits evolution and generates erratic population abundances that never can fully reach either the ESS or the TEA. At lower density dependence and higher population sizes, however, the populations can more smoothly find their way toward the ESS.

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Figure 4. Results of Gillespie eco-evolutionary model (GEM) simulations of the birth-death logistic model for populations culled to five individuals from the starting point at the ESS trait and the equilibrium abundance. From left to right, the population is culled more severely (to 100, 50, and 5 from left to right). Layout the same as in Figure 2.

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Figure 5. Transient fitness landscapes for the birth-death logistic model with three levels of culling and the weakest density dependence (*b*s = *d*s = 0.01). The overall layout is the same as in Figure 3. The colored lines represent the trajectories from Figure 4, with orange being a cull to 100, purple being a cull to 50, and green being a cull to 5 individuals. Each population is evolving toward their local TEA (color coded to match trajectories). The populations started at the ESS trait and equilibrium abundance (blue dot).

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Figure S1. Results of a GEM simulation of the birth-death logistic model evaluating the isolated effects of trait variance on the dynamics. In these simulations, variance in the linked birth and death rates were isolated, and heritability was set to zero. In the leftmost panel, all trait variance was removed, causing the simulations to collapse on the non-evolutionary ordinary differential equation solution. This indicates that the GEM effectively collapses to a standard Gillespie simulation. In the second panel from the left, variance in mortality was removed by setting it equal to the mean value given its link to births (see main text). In the third panel, the reverse removed variance in births while retaining in deaths. In the fourth panel, variance in both traits was retained. This final panel indicates that trait variance (demographic heterogeneity) alters the ecology of the system, lowering the abundance at equilibrium relative to that expected from the mean traits themselves.

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