**Stochasticity directs adaptive evolution toward transient evolutionary attractors**

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**Abstract**

Stochastic processes such as genetic drift may overwhelm selection and hinder adaptation, but the effect of such stochasticity on evolution via its effect on ecological dynamics is poorly understood. Here we evaluate patterns of adaptation in a population subject to both environmental and demographic stochasticity. We show that stochasticity can alter population dynamics and lead to evolutionary outcomes that are not predicted by classic eco-evolutionary modeling approaches. We also show, however, that these outcomes can be understood as being governed by transient evolutionary attractors (TEAs) – these are fitness maxima when the ecological system is not at equilibrium. These TEAs alter the path of evolution but are not visible through an equilibrium lens. We further show that trait-independent culling can redirect evolution away from expected evolutionary equilibria and toward these TEAs. Our results reveal that considering the path toward adaptation during transient periods can greatly improve our understanding of the path and pace of evolution.

**Introduction**

Debates over the effects of stochasticity on ecological and evolutionary dynamics go back to foundational work in ecology and evolutionary biology, from Fisher’s and Wright’s contrasting views of the role of mutation and drift (Fisher 1930; Wright 1931) to Nicholson’s and Andrewartha and Birch’s differing opinions about whether populations were primarily regulated by density-dependent or density-independent (e.g., stochastic) processes (Andrewartha & Birch 1954; Nicholson 1957). Mathematical models have proven to be a valuable tool for studying the various ways that stochasticity can impact ecological (reviewed in Coulson *et al.* 2004; Black & McKane 2012) and evolutionary (reviewed in Lenormand *et al.* 2009) dynamics. For example, evolutionary theory has revealed the potential for genetic drift to facilitate adaptation (Wright’s “shifting balance” theory; Wright 1931, Coyne et al. 1997) and how stochasticity can shape life history evolution (e.g., “bet hedging” strategies; (Cohen 1966; Childs *et al.* 2010; Rees & Ellner 2019). Ecological theory has shown how stochasticity can excite an underlying deterministic tendency for a system to oscillate, leading to sustained oscillations (Greenman & Benton 2003; McKane & Newman 2005), and how it can cause systems to shift between different deterministic attractors (Henson *et al.* 1998; Ives *et al.* 2008; Ashwin *et al.* 2012; Abbott & Nolting 2017). However, despite this long-standing interest, there is a need for additional work studying how stochasticity affects evolutionary dynamics *through* its effects on ecological dynamics.

A number of theoretical approaches for studying the interplay between ecological and evolutionary dynamics have been proposed (reviewed in (Abrams 2001), including quantitative genetics (QG) and adaptive dynamics (AD) approaches (Abrams *et al.* 1993b; Dieckmann & Law 1996; Geritz *et al.* 1998; Abrams 2001). While there are important differences between the two methods, for example in their assumptions about reproduction and the relative timescales of ecological and evolutionary processes, their predictions for eco-evolutionary dynamics are often identical. This is because, in both approaches, the direction of selection is determined by the fitness gradient: the derivative of individual fitness () with respect to the evolving trait (). The dynamics of the mean trait () are given by (Abrams *et al.* 1993b; Abrams 2001; Doebeli *et al.* 2017):

An equation of this form can be arrived at either through the equations for trait change in quantitative genetics (Lande 1976; Abrams *et al.* 1993b) or through a consideration of stochastic birth-death processes (Dieckmann & Law 1996). Given that individual fitness will be affected by ecological interactions, there is broad scope for eco-evolutionary feedbacks to affect the dynamics of both the ecological and evolutionary system in non-intuitive ways (Fussmann *et al.* 2003; Cortez & Ellner 2010; Vasseur *et al.* 2011; Cortez 2016; Lowe *et al.* 2017).

Given the key role of ecological dynamics in shaping the fitness gradient, stochasticity that alters ecological dynamics also may influence adaptation (Start *et al.* 2020). However, both the QG and AD approaches typically assume that populations are large so that demographic stochasticity (random variation in the sequence and number of demographic events) can safely be ignored. Studies that have included demographic stochasticity have shown that it can alter the eco-evolutionary dynamics predicted by QG and AD approaches (Proulx & Day 2002). For example, demographic stochasticity can affect the dynamics of adaptation through genetic drift (Lenormand *et al.* 2009), the loss of high-fitness genotypes (Crespi 2000), delaying or preventing evolutionary branching due to disruptive selection (Claessen *et al.* 2007; Wakano & Iwasa 2013), or leading to the evolution of pathogens with lower transmission and virulence (Humplik *et al.* 2014; Parsons *et al.* 2018).

In addition, (differences in expected demographic rates among individuals) may influenceevolutionary outcomes through two mechanisms, which is known as individual demographic stochasticity

To study how stochasticity can influence the path and pace of adaptation by altering ecological dynamics, we use Gillespie eco-evolutionary models [GEMs] (DeLong & Gibert 2016; DeLong & Luhring 2018; DeLong & Belmaker 2019), to generate the ecological and evolutionary dynamics through the simulation of stochastic birth-death processes (Dieckmann & Law 1996; Champagnat *et al.* 2006; Doebeli *et al.* 2017). Specifically, we compare the ecological and evolutionary dynamics produced by GEMs to deterministic expectations based on the quantitative genetics (QG) approach (Lande 1976; Abrams *et al.* 1993b). Demographic stochasticity is built into the structure of the GEMs through stochasticity in the birth and death process. We study the eco-evolutionary dynamics of a simple ecological model of logistic growth in two scenarios: 1) varying the location of the ecological equilibrium (i.e., carrying capacity) and 2) introducing culling that is unrelated to an individual’s traits. We show that demographic stochasticity often prevents populations from reaching the expected evolutionary equilibrium, but we find that the realized evolutionary outcome can still be understood using the deterministic equations. In particular, we show that stochasticity can trap populations at “transient evolutionary attractors” (TEAs), which we define as density-dependent fitness optima that are temporary because they change location as the population grows or declines. We suggest that these TEAs may play an important role driving evolutionary dynamics in many natural systems, and more generally, that understanding transient evolutionary phenomenon may provide new insights into how populations evolve.

**Material and methods**

*Deterministic eco-evolutionary dynamics:* The quantitative genetics approach to modeling eco-evolutionary dynamics allows for ecological and evolutionary dynamics to occur on similar timescales (Abrams 2001). The QG approach derives the fitness gradient equation as an approximation of the quantitative genetics equations of Lande (1976) that assume that the trait distribution is unimodal and that the variance in fitness is greater than the variance in the trait (Taper & Case 1992; Abrams *et al.* 1993a, b; Abrams 2001). An identical expression also can be derived from the dynamics of genotypes via the Price equation (Taylor & Day 1997; Day & Gandon 2006). The rate of evolutionary change is also affected by the additive genetic variance; this value is often held constant but can be allowed to change dynamically (Abrams et al. 1993b, Taylor & Day 1997).

To investigate how stochasticity influences evolutionary dynamics, we consider a simple model for density-dependent population growth that can provide deterministic baseline expectations:

, (Equation 1)

where *R* is population abundance, *bmax* is the maximum birth rate, *dmin* is the minimum death rate, and *bs* and *ds* characterize the effects of population abundance on the realized birth and death rates, respectively. This model is a simple expansion of the logistic model, with maximum rate of population growth given as *rmax* = *bmax* - *dmin* and a carrying capacity defined as . We redefine the logistic model this way to allow us to simulate the ecological dynamics as a stochastic birth-death process (Doebeli *et al.* 2017). We choose a logistic-type model as an approximation of the sigmoidal population growth dynamics shown by a variety of organisms in relatively simple scenarios (Gause 1934; Sibly *et al.* 2005; Lee *et al.* 2018).

We consider the case where *bmax* is evolving and is connected to mortality through a classic life history trade-off between reproduction and mortality (Stearns 1976; Reznick *et al.* 2000). This trade-off has been widely demonstrated across plants, invertebrates, and vertebrates (Lee *et al.* 2008; Wilder *et al.* 2013; Hosking *et al.* 2019); more practically, positing such a trade-off facilitates our analysis because it leads to an evolutionary equilibrium where fitness is maximized. Using the QG approach, the dynamics of the population mean trait, , are given by

where *V* is the product of narrow-sense heritability and additive genetic variance in *bmax,* is the per-capita growth rate (i.e., individual fitness), andis the fitness gradient evaluated at the mean trait. The fitness gradient will equal zero at the evolutionary equilibrium. Given equation (1) above, the fitness gradient is equal to , which implies that the minimum death rate must be an increasing function of the maximum birth rate for an evolutionary equilibrium to exist. For any equilibrium to represent a fitness maximum requires which implies that the minimum death rate must be an accelerating function of maximum birth rate. As such, we assume that , making the equation for the evolutionary dynamics

(Equation 2)

Thus, in the deterministic QG model given by equations (1-2), the population will approach the eco-evolutionary equilibrium:

. (Equation 3)

We borrow the terminology of the adaptive dynamics literature and call this value of an evolutionarily stable strategy (ESS), since it is an evolutionary equilibrium where fitness is maximized.

*Stochastic eco-evolutionary dynamics:* GEMs simulate ecological dynamics through a stochastic birth-death process (DeLong & Gibert 2016; DeLong & Luhring 2018; DeLong & Belmaker 2019). GEMs build on the standard Gillespie algorithm for simulating ODE models where demographic stochasticity (random variation in the sequence and number of demographic events) influences the outcomes (Gillespie 1977; Yaari *et al.* 2012) and by incorporating demographic heterogeneity (variation among individuals in expected demographic traits). Every individual in the simulation has a trait value drawn from a distribution with known mean and variance, with the type of distribution depending on the nature of the trait (here we assume a lognormal distribution since can only take positive values). In a GEM, an individual’s trait value determines its probability of giving birth or dying; evolutionary dynamics thus emerge out of the stochastic births and deaths of individuals within the population (Dieckmann & Law 1996; Champagnat *et al.* 2006; Doebeli *et al.* 2017)

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 (Appendix S1). 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 likelihood 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.

*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, variation in *b*max will drive variation in *d*min. We therefore broke this apart to evaluate the effect of variation in each parameter on ecological dynamics separately. We examined whether variation in neither trait, *b*max alone, *d*min alone, or both traits combined, influenced the dynamics, respectively, by eliminating variation altogether; by allowing variation in *b*max but holding *d*min constant; by allowing variation in *d*min but holding *b*max constant (achieved by first allowing variation in *b*maxto drive variation in *d*min but then re-setting *b*max to the mean); and by allowing both to vary together as normal. This examination also confirmed that the GEM dynamics reduced to a standard Gillespie simulation of the ecological model (Equation 1). We used *b*s = *d*s = 0.04 for this simulation.

Comparison 2: We next evaluated differences between the GEM and QG 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. 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. We checked whether our results were qualitatively similar if we used different parameter values, specifically, whether the choice of the trade-off constant (*c*, above) altered the outcomes.

Comparison 3: We next asked how culling a population that has already achieved an eco-evolutionary equilibrium would cause it to evolve when the probability of death due to the cull was independent of an individual’s traits. The deterministic model for the population dynamics for the birth-death logistic model with an additional culling term is the following:

Under this model, we cull the population at the rate whenever . As , the equilibrium . As we show in Appendix S2, because this culling is trait-independent, the evolutionary dynamics for the mean trait are still given by equation (2) above. We do this with an intermediate level of density dependence with three levels of culling.

*Modeling details:* For Comparisons 1 and 2, populations were initialized with five individuals with mean traits and *c* = 0.0926 (since , ). The ESS *b*max for this system is 5.4, which means the ESS *d*min is 2.7. The CV of the evolving trait in the initial population was set at 0.3, such that the initial variance in *b*max was 0.29. Heritability was fixed at 0.75. We make density dependence in births and deaths symmetrical, so *b*s = *d*s, and set these equal to 0.075, 0.0375, and 0.0187 to generate a gradient in density dependence. Since the equilibrium abundance depends on the value of *bmax* (Equation 3), the initial carrying capacities at *bmax*=1.8 were 10, 20, and 40 across the three scenarios; at the ESS value of *bmax*=5.4, the equilibrium abundances were 18, 36, and 72. For a check on the effect of different parameter values, we also varied *c* (0.06, 0.09, and 1.2), using *bmax* = 1.8 and one level of density dependence (). For Comparison 3, populations were initialized with 72 individuals with (thus at the eco-evolutionary equilibrium for ). Individuals were culled at random with respect to their traits with a culling rate of (which ensures that the population size rapidly approaches ) and values of 50, 30, or 10. We ran each simulation long enough to clearly identify its attractor, which was 50 for comparisons (ecology only) and 400 for all subsequent eco-evolutionary simulations. We replicated each stochastic simulation 50 times.

To evaluate patterns in individual fitness across GEM simulations, we tracked the number of reproductive events and the lifespan for each individual. This allowed us to visualize the realized relationship between each individual’s *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 350). For the latter, we only included individuals that died before the end of the simulation.

**Results**

*Comparison 1:* In the first comparison, we sought to determine if individual variation altered population abundance relative to the expected equilibrium abundance. Reducing heritability to zero effectively eliminates evolution by natural selection, revealing how trait variation *per se* alters the dynamics of the system (Figure 2). Variation in either *b*max or alone had little effect on population abundance compared to the expectation, but when *b*max and *d*min were allowed to vary together, as specified by our trade-off function, the equilibrium abundance of the population was reduced by about 7% below the expected equilibrium. This is actually an expected result: in the absence of any trade-off, the equilibrium abundance is a linear function of either or , but when they are allowed to vary according to the trade-off, is a nonlinear function of , and nonlinear averaging would cause a decrease in population abundance due to Jensen’s inequality (Hart *et al.* 2016). This result indicates that trait variation *per se* is one factor that may limit the populations in our simulations from achieving the expected ecological equilibria.

*Comparison 2:* In our second set of simulations, we sought to determine whether the stochasticity generated by low population size altered evolutionary outcomes. In this comparison, we varied only the strength of density dependence, and we found that all populations grew towards the expected ecological equilibrium and *b*max evolved towards the ESS (Figure 3, 1st, 2nd, and 5th rows). Although no population was able to grow or evolve as fast as expected from QG (Figure 3, 1st and 2nd rows), the population experiencing the least density dependence converged to the expected eco-evolutionary equilibrium. The depiction of the eco-evolutionary dynamics in the phase plane (Fig. 3, row 5) is also illustrative: the initial ecological dynamics are much faster than the evolutionary dynamics (the initial movement in the phase plane is mostly in the direction of increasing population abundance), and then both abundance and the trait increase together towards the eco-evolutionary equilibrium given by the orange point (Fig. 3, 5th row).

We also found that populations with stronger density dependence (i.e., higher values of *bs* and *ds* and therefore lower values) experienced greater initial loss of trait variation (Figure 3, third row). This loss of variation slows the pace of evolution relative to the QG expectation. At intermediate and low density dependence (higher ), the initial loss of trait variation was more temporary, allowing populations to recover from the effects of low-density stochasticity and continue moving in the direction of the ESS. As expected, 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 3, left column). However, all populations displayed considerable individual demographic stochasticity (Figure 3, 4th row), manifested as large differences in lifetime reproductive success among individuals with the same trait values. In addition, there was considerable demographic heterogeneity in the populations even after the distribution of *b*max values had centered on the optimal values.

It is also clear that the evolutionary dynamics often do not reach the expected evolutionary equilibrium, especially in small populations where demographic stochasticity is especially strong. In particular, the median of the stochastic trajectories often settles onto a trait value that is noticeably smaller than the ESS (Fig. 3 row 2 and 5). To help understand this result, we calculated the expected lifetime reproductive success (LRS) of an individual from the model:

(Equation 4)

The value of *bmax* that maximizes LRS is given by the solution of the equation:

(Equation 5)

Note that the value of *bmax* that maximizes expected lifetime reproductive success is not necessarily the same as the ESS value (although when *R* is at an equilibrium, the values are the same). In particular, this value depends on the current population size. We term this transient peak on the fitness landscape a “transient evolutionary attractor” (TEA), because it changes as the population moves through its transient dynamics. Re-examining the observed lifetime reproductive success values, it is clear that the peak of the observed distribution is often centered on these TEAs (Fig. 3, 4th row), and that the observed evolutionary trajectory for *bmax* often appears to be approaching this TEA, rather than the ESS (Fig. 3, 2nd and 5th rows). The outcome in which populations evolved toward a TEA rather than an ESS holds across a range of values for the trade-off slope, *c* (Figure S5).

*Comparison 3:* In our third set of simulations, we sought to understand whether an external force altering population size would drive evolution away from the expected ESS. Here we applied a persistent cull to populations that had already achieved their ESS trait and abundance values. The population size changed almost immediately so that , while the evolutionary trajectory showed a clear movement of the mean away from the ESS. Again, we can ask what value of maximizes expected reproductive success. The expected lifetime reproductive success under culling is

(Equation 6)

Assuming that , the value of that maximizes LRS is given by Eq. (5) above. Fig. 4 shows clearly that the population mean evolved to the population-specific TEAs that depended on the population size the cull produced (Figures 4,5). Rather than returning to the ESS, populations that were culled to a lower abundance shifted their path immediately to head upslope toward the abundance-determined TEA and away from the ESS (Figure 5). The populations followed a path of adaptation specific to the current transient 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.* 1993a; DeAngelis & Mooij 2005; Coulson *et al.* 2006; Ellner & Rees 2006; Lion 2017; de Vries & Caswell 2019; Govaert *et al.* 2019). (Doebeli *et al.* 2017) has argued that the mechanistic foundation for evolutionary theory should be stochastic birth-death processes, rather than fitness. However, while such models can readily be simulated, as we do here, deterministic approximations of such processes are required to make limiting assumptions, such as a separation of ecological and evolutionary timescales, weak selection, small mutation, or large population size (Dieckmann & Law 1996; Champagnat *et al.* 2006; Doebeli *et al.* 2017; Parsons *et al.* 2018). Here we show two important results. First, when populations are large, the deterministic approximations can provide an accurate description of both the transient and equilibrium behavior of the ecological and evolutionary dynamics (Fig. 3, right column). This is expected, since the assumption of large population sizes is included in most classic evolutionary theory, but is still reassuring. Second, even when these limiting assumptions are not met and the stochastic eco-evolutionary dynamics do not exactly match the deterministic expectation, the deterministic equations can still be useful in helping to understand the resulting eco-evolutionary dynamics. In particular, we show that demographic heterogeneity and demographic stochasticity can keep populations away from an expected ecological equilibrium, and that under such conditions the population mean traits can evolve towards transient evolutionary attractors. 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, such as classic adaptive dynamics approaches that assume a separation of ecological and evolutionary timescales (Geritz *et al.* 1998; Abrams 2001). 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 that disrupts populations throughout the world today, we agree that theories of evolution that focus on stochastic birth-death processes, and the transient, non-equilibrium dynamics of such processes, 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 that the presence of individual trait variation (and the resulting demographic heterogeneity; (Kendall *et al.* 2011; Stover *et al.* 2012), although required for evolution to proceed, can itself change the ecological dynamics. In our case, this variation simultaneously facilitated evolution by providing raw material upon which selection could act and maintained the system in a transient state (i.e., a state in which equilibrium has not been attained) such that the expected evolutionary equilibrium could not be attained. Individual demographic stochasticity, abundantly displayed in our results, clearly influenced the relationship between fitness and traits, causing some individuals with low fitness traits to realize high fitness, while some individuals with high fitness traits to realize low fitness (Figures 3 and 5, bottom row). This effect should result in a flattened fitness gradient relative to the expectations from quantitative genetics, greatly reducing the rate of evolution and maintaining individual variation (Cressler *et al.* 2017). Finally, demographic stochasticity generated heightened variation in population size for small populations, both keeping populations in transient states and leading to substantial initial loss of genetic variation. Examination of the population dynamics in the systems with lower carrying capacities (Figure 3) indicate substantially more variation in population sizes, reflecting high stochasticity. All together, these forces substantially slowed evolution relative to expectations generated from classic assumptions of deterministic evolutionary theory.

Increasing evidence indicates that ecological dynamics can play a crucial role in shaping evolution (Pimentel 1961; Grant & Grant 2002; Yoshida *et al.* 2004; Hairston *et al.* 2005; Schoener 2011). Furthermore, evolution within systems not at equilibrium, and rather displaying transient dynamics (Hastings *et al.* 2018), can alter the ecological dynamics and therefore the selective forces acting on the population (Fussmann *et al.* 2003; Yoshida *et al.* 2003; Cortez & Weitz 2014). Our results further this finding, demonstrating that even simple, single-species models can facilitate not just eco-evolutionary dynamics but generate transient attractors (TEAs) that may compete with the overall evolutionary attractor in the system (the ESS). By taking into account the full consequences of individual variation and stochasticity, we may generate more realistic predictions for evolution. We do not, however, suggest that TEAs will be present in all systems. The minimum requirement for a TEA is that the expression must actually have a solution, otherwise there is neither an ESS nor a TEA. Furthermore, if an expression for a trait optimum includes population size, then the optimum is not the same at equilibrium as it is away from equilibrium. The non-equilibrium peak is the TEA, and the equilibrium peak is the ESS. In our Equation 5, a fitness maximum exists and population abundance *R* is present in the expression, generating a TEA. Thus, to the extent that these conditions are met, likely in most cases of density-dependent demographics with some sort of trade-off among fitness related traits, TEAs may be a common feature of evolutionary pathways.

One of the most non-intuitive results here is that culling can dramatically alter the evolutionary dynamics from the expectation. As we show in Appendix S2, trait-independent culling does not alter the expected evolutionary dynamics, and thus we would expect that a population whose trait was already at the ESS would not evolve away from it. And yet, we see that trait evolution moves away from the ESS and towards the TEA (Fig. 5) when the population is culled. Our results may have important 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 evolutionary outcome 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. Culling our simulated population nearly halved the fecundity of the population, even without it having a direct selective effect (as captured by the equation for the evolutionary dynamics). This would have long-term ramifications for the culled population, as the ecological equilibrium would not quickly return to the pre-cull levels upon relaxation of the cull.

Studying the evolutionary process from the perspective of stochastic birth-death processes increases the opportunity for profitable cross-pollination between ecological and evolutionary theory (Doebeli *et al.* 2017). In particular, while other authors have used approaches very similar to GEMs to test the predictions of classic evolutionary theory (e.g., (Claessen *et al.* 2007), GEMs provide a natural and straightforward way to reformulate classic ecological models into stochastic evolutionary birth-death processes (DeLong & Gibert 2016; DeLong & Luhring 2018; DeLong & Belmaker 2019), allowing ecologists and evolutionary biologists to study the feedback between ecological and evolutionary dynamics that emerges out of such a reformulation.

In conclusion, our results indicate that stochastic birth-death processes, by introducing individual variation and demographic stochasticity, can produce evolutionary trajectories that differ significantly from expectations based on deterministic approaches, revealing powerful competing evolutionary attractors (TEAs) that have not factored into much (if any) current thinking about the pace and path of adaptation. However, we also find that these TEAs can still be understood on via the deterministic approximations, helping to reveal both the utility and the limitations of such approximations. 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 & Thompson 1987). These data show that lifetime reproductive success (here lifetime clutches) may reach a peak at some intermediate trait value (near 4.1 mm). Simultaneously, individuals may vary dramatically in their realized fitness despite an expected fitness outcome.

Figure 2. Results of a GEM simulation of the birth-death logistic model evaluating the isolated effects of trait variation on the dynamics. In these simulations, variation in the linked birth and death rates were isolated, and heritability was set to zero. In the leftmost panel, all trait variation 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, variatoin in mortality was removed by setting it equal to the mean value given its link to births (see main text). In the third panel, we removed variation in births while retaining it in deaths. In the fourth panel, variation in both traits was retained. This final panel indicates that trait variation (demographic heterogeneity) alters the ecology of the system, lowering the abundance at equilibrium relative to that expected from the mean traits themselves. The median (dark solid line) and middle 50% (shaded area) of 50 simulations are shown.

Figure 3. Gillespie eco-evolutionary model (GEM) simulations of the birth-death logistic model. The rows show from top to bottom population abundance, mean *b*max, variance in *b*max, lifetime reproductive success (product of expected births and expected lifespan), and the mean trajectory through the abundance- *b*max phase plane. The columns show three levels of density dependence in birth and death rates (values of *b*s and *d*s) that set the initial carrying capacity at 10, 20, and 40 from left to right. (The initial carrying capacity is the ecological equilibrium if *b*max remained fixed at 1.8.) The median and middle 50% of 50 stochastic GEM trajectories are in purple and light purple, respectively. The quantitative genetics (QG) expectation is in bold orange. The difference between the evolutionary stable strategy (ESS) and the transient evolutionary attractors (TEAs) can be seen by comparing the dashed orange and pink lines in the second row. Lifetime reproductive success as a function of *b*max is shown for individuals that were born and died within the last 20 timesteps. The evidence that the population evolves toward the TEA is the convergence of the purple line in the second row with the dashed pink line and by looking at the phase portrait in the fifth row.

Figure 4. Results of Gillespie eco-evolutionary model (GEM) simulations of the birth-death logistic model for populations culled from a starting population at the ESS trait () and the equilibrium abundance (72 individuals). From left to right, the population is culled more severely (to 50, 30, and 10 from left to right). Layout the same as in Figure 3 with 50 replicate simulations. The evidence that the population evolves toward the TEA is the convergence of the purple line in the second row with the dashed pink line.

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 5, 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).

Figure 1.

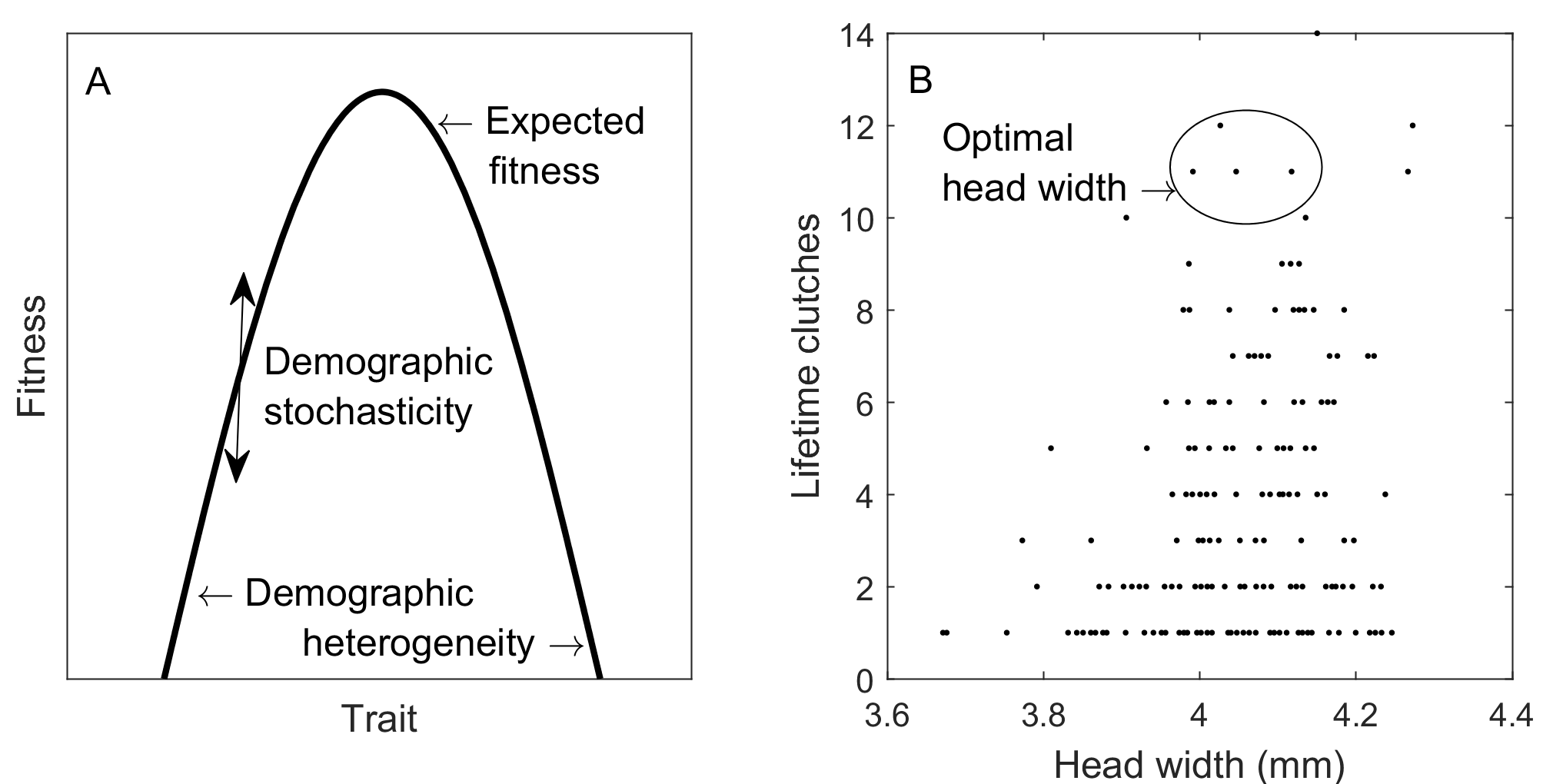


Figure 2.

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Figure 3.



Figure 4.

Figure 5.

**DeLong and Cressler, “Transient evolutionary attractors alter evolutionary adaptation”**

**Appendix S1. Heritability rules.**

In a GEM, births and deaths occur through an iterative, stochastic process given an underlying model. In the event of 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 derived and presented in (DeLong & Luhring 2018; DeLong & Belmaker 2019) with the change that we are not using here the weighted mean for the parental trait.

If a birth event occurs in a GEM, 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, is the current population mean, and *h*2 is narrow-sense heritability. The standard deviation of this distribution is given as , where is the standard deviation in *b*max in the initial population and is the standard deviation in *b*max currently. This trait is then added as a new element of the trait distribution, increasing the size of the population by one and changing the mean and variance of the trait distribution.

This rule is derived from the equation of the regression line in a parent-offspring regression (DeLong & Belmaker 2019). To verify that the realization of this rule in a GEM implementation generates a parent-offspring regression with an estimated *h*2 that matches what was set in the model, we track parent and offspring traits through GEMs initialized with different *h2* values (0.9, 0.7, 0.5, and 0.3). Using simple linear regression of offspring traits on parent traits, we verify that the estimated *h2* (the slope of the regression) remains close to the expected *h*2 (Fig. S1-S4).

Over any short interval of time in a GEM run, the realized parent-offspring relationship behaves as expected. After accumulating observations over longer runs, however, we see that the *h*2 appears to converge on one. This is also expected: as the population evolves, the parent and offspring traits move in phenotypic space (as you can see from the changing x- and y-axis ranges in Figs. S1-S4), “smearing” the parent-offspring regressions (each of which has a slope of *h2* at any one moment in time) into a parent-offspring regression that has a slope approaching one.



Fig. S1. Parent-offspring regressions through time when *h2* = 0.9.



Fig. S2. Parent-offspring regressions through time when *h2* = 0.7.



Fig. S3. Parent-offspring regressions through time when *h2* = 0.5.



Fig. S4. Parent-offspring regressions through time when *h2* = 0.3.

**DeLong and Cressler, “Transient evolutionary attractors alter evolutionary adaptation”**

**Appendix S2. Deriving the evolutionary dynamics for the ecological model with culling**

Consider the following ecological model:

where is a function of .

We will consider two ways of deriving the evolutionary dynamics.

In the first, we follow the approach of (Day & Gandon 2006) and derive an exact model for the evolutionary system. Let us consider our population-level model to a model of *n* “genotypes”, . The dynamics of each genotype are given by the equation:

where and are the birth and death rate of this genotype, is the total population size, and gives the probability that individuals of this genotype will be among those culled if the total population size is larger than (alternatively, you can interpret as the relative rate of culling of ).

Absent any process of mutation (e.g., if heritability was perfect), this is a full description of the evolutionary dynamics of the system. The model could be extended to consider mutation between genotypes (or the creation of new genotypes). However, the above system describes selection among the genotypes, which is the key process which we wish to derive here.

We will change variables to track the frequencies of each genotype, . Then the dynamics of this frequency will be given by

The dynamics of total population size, , are given by

The sums and are just the average values and across all genotypes.

Then the frequency dynamics are given by

Thus, the frequency of each genotype depends on the difference between this genotype’s per-capita birth and death rates and the population average birth and death rates. Specifically, if the difference between the maximum birth and minimum death rates for this genotype is larger than the population average, the genotype will increase in frequency.

Given this equation for , we can derive an equation for the dynamics of the average trait, :

This latter expression is the covariance between and across all strains; that is,

This is Price’s equation (Day & Gandon 2006). Assuming normality of the phenotype distribution, (Taylor & Day 1997) show that the covariance is proportional to the product of the additive genetic variance and fitness gradient (the derivative of individual fitness with respect to the individual trait (Abrams 2001), implying that the evolutionary dynamic can be written as

Since , and the evolutionary dynamic in the model with culling is identical to the evolutionary model without culling.

Note: GEMs actually assume that the trait is actually *lognormally* distributed, to prevent negative trait values. This modifies the above derivation only slightly. In particular, , so the trait dynamics would be given by:

Thus the direction of evolution (and equilibrium) of a lognormally distributed trait will be identical to that of a normally distributed trait, although the rate will differ because of the normalization by the mean trait.

We can also show this using more of an adaptive dynamics approach. That is, consider the invasion of a mutant with a different value into a monomorphic resident population. Let and be the mutant and resident trait values, respectively. Then the dynamics of the two populations are given by

If we assume that the mutant is attempting to invade from rarity (so ), then whether is will be able to invade will be given by the stability of the equilibrium The stability can be assessed with the Jacobian matrix

Since this matrix is upper-triangular, the eigenvalues are given along the diagonal. The first eigenvalue determines the stability of the system when the mutant is absent, and we can assume it is negative. Therefore, the mutant can invade if the following is satisfied:

The quantity is often termed the “invasion fitness” (Geritz *et al.* 1998), and the derivative of this expression with respect to the mutant trait , evaluated at the value (consistent with the adaptive dynamics assumption that mutations are small), determines the direction of selection. It is clear that . This is identical to the expression derived above, as expected given that the fitness gradient expressions between QG and AD approaches are often identical (Doebeli *et al.* n.d.; Abrams *et al.* 1993; Dieckmann & Law 1996; Taylor & Day 1997; Abrams 2001). This serves as further confirmation that the evolutionary equilibrium will be independent of culling.

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