Debates over the effects of stochasticity on ecological and evolutionary dynamics go back to some of the foundational work in both ecology and evolutionary biology, from Fisher’s and Wright’s contrasting views of the role of mutation (Fisher 1958, 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 (Nicholson 1957, Andrewartha & Birch 1954). 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. 2008) dynamics. For example, evolutionary theory has revealed the potential and limitations of 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; ; Ecological theory has shown how stochasticity can excite an underlying deterministic tendency for a system to oscillate, leading to sustained oscillations (Greenman and Benton 2003, McKane and Newman 2005), and how it can cause systems to shift between different deterministic attractors (Henson et al. 1998, Ashwin et al. 2012). However, despite this long-standing interest, there has been little work studying how stochasticity affects evolutionary dynamics *through* its effects on ecological dynamics.

However, it is intuitive that such effects must exist. Adaptation, in particular, is often visualized using a fitness landscape where peaks represent locally optimal trait values, and where the “shape” of the landscape is determined by ecological interactions (Wright 1931). Classical approaches to identifying such peaks typically start by assuming an ecological equilibrium and asking what traits maximize fitness at this equilibrium (Lande 1976, 1982; Abrams et al. 1993a). This approach is fundamental to a wide range of theoretical work aimed at understanding the process of adaptation (Fussmann et al. 2003, Cortez & 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 fitness, thereby changing the shape of the fitness landscape and the location of adaptive peaks (Govaert et al. 2019). In particular, the fitness landscape becomes dynamic, with peaks moving dynamically through trait space. These feedbacks can be quite rapid, since the timescales of ecology and evolution are not as different as is typically assumed (Hairston et al. 2005, Schoener 2011, DeLong et al. 2016). In a now-classic example, selection fluctuated between favoring grazing-resistant and rapidly growing algae genotypes due to cycles of grazing activity by rotifers (Yoshida et al. 2004). Such fluctuations dictate that the relationship between traits and fitness will change rapidly through time, such that a population evolves in one direction, and then another, as the ecological context changes.

Stochasticity, therefore, has the potential to affect selection by modifying the ecological dynamics, keeping the evolving population away from its deterministic attractor. We can distinguish different kinds of stochasticity that can affect ecological and evolutionary dynamics. Demographic stochasticity is random variation in realized vital rates among individuals that are deterministically identical; demographic stochasticity leads to genetic drift, which is typically understood to function as a brake on adaptive evolution by reducing the probability of fixation of beneficial alleles (Haldane 1927, Crespi 2000). Environmental stochasticity is random variation in the environment that affects the vital rates of all individuals in a population. One often-overlooked source of environmental stochasticity present in all numerical analyses is the choice of initial conditions. The choice of initial conditions determines the transient dynamics of the system; these transients can sometimes be very long (e.g., in Lotka-Volterra competition models, the system can often spend a considerable amount of time near the unstable coexistence equilibrium before moving towards a stable single-species equilibrium; Hastings 2004). As such, transient dynamics may often be an important source of environmental stochasticity that can shape evolutionary dynamics. Given that most populations experience demographic and environmental stochasticity, and thus do not typically reside at an ecological equilibrium, it is crucial to consider how our expectations for evolution could be altered by stochasticity.

To study how stochasticity can influence the path and pace of adaptation by altering ecological dynamics, we use a novel theoretical approach that adds individual variability and inheritance to a stochastic simulation of ecological dynamics using Gillespie’s direct method for simulating stochastic systems (Gillespie eco-evolutionary models [GEMs]: DeLong and Gibert 2016, DeLong and Lurhing 2018, DeLong and Belmaker 2019). Specifically, we compare the ecological and evolutionary dynamics of GEMs to deterministic expectations based on the quantitative genetics (QG) approach of Lande (1982) and Abrams et al. (1993). Demographic stochasticity is built into the structure of the GEMs through stochasticity in the birth and death process. Environmental stochasticity via transient dynamics is introduced 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. We show that stochasticity limits adaptation, preventing populations from reaching the expected evolutionary optimum, but 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). These TEAs represent peaks on an adaptive landscape that is not identical to the deterministic expectation. 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.

**Methods**

*Deterministic eco-evolutionary dynamics:* Lande (1976, 1982) derived an expression for the dynamics of trait change from classical quantitative genetics, showing that the average trait in a population changes at a rate that is proportional to the gradient of fitness with respect to the trait. This approach was generalized to allow for ecological interactions to shape the fitness gradient (Taper and Case 1992, Abrams et al. 1993A, 1993b, Abrams and Matsuda 1997), thus defining an eco-evolutionary model. The timescale of evolutionary change, relative to ecological change, depends on the amount of genetic (co)variance in the population (Lande 1976). Typically, this term is small, leading to a rough separation of timescales where ecological dynamics happen faster than evolutionary dynamics. However, the relative rate of evolutionary dynamics can be scaled by other factors to alter the separation of timescales between the two dynamics; recent work has shown that allowing evolutionary dynamics to be faster than ecological dynamics can have non-intuitive effects on both ecology and evolution (Cortez and Ellner 2010; Cortez 2016). One of the key takeaways from all of this work is that the dynamics of the system tend to be determined much more by the dynamics of the faster subsystem (Cortez and Ellner 2010). Thus, typically, that means that the system will move quickly to an ecological equilibrium that will itself change slowly as the mean trait changes. Under this view, then, the transient behavior of the ecological system will have very little effect on the path to adaptation.

Here we consider this simple model for density-dependent population growth:

, (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. We consider the case where *bmax* is evolving and is connected to mortality through a trade-off described by an accelerating function,

Using the QG approach, the dynamics of the population mean trait, are given by

where *V* is the additive genetic variance in *bmax,* is per-capita growth rate (fitness), and is the selection gradient. Evaluating that derivative, the equation is

(Equation 2)

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

. (Equation 3)

This value ofis an evolutionarily stable strategy (ESS) that maximizes fitness.

*Stochastic eco-evolutionary dynamics:* 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 is the standard deviation in *b*max in the initial population and is the standard deviation in *b*max currently. 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; in particular, when populations are small and there is less variation, there will also be less difference between parents and offspring. 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, 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).

*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 bmax on the ecological dynamics of this model when no evolution was possible. To do this, we set heritability h2 = 0 and introduced variation in traits in the population with CV = 0.3. Because in our model, the dmin is locked to bmax, we examined whether variation in neither trait, bmax alone, dmin 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 ecological model (Equation 1).

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.

Comparison 3: Finally, we asked how harvesting a population that has already achieved an ESS trait and ecological equilibrium would cause it to evolve. Here harvesting is functioning as a form of environmental stochasticity, since individuals are removed from the population irrespective of their trait values. 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 *s* = 0.0926. Heritability was fixed at 0.75. 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. Since the equilibrium abundance depends on the value of *bmax* (Equation 3), the initial equilibrium abundances at *bmax*=1.8 were 7.5, 15, and 75 across the three scenarios; at the ESS value of *bmax*=5.4, the equilibrium abundances were 13.5, 135, and 1350. For Comparison 3, populations were initialized with 135 individuals with (thus at the ESS for ). Individuals were randomly culled to maintain the populations at a size of 100, 50, or 10. We ran each simulation for 60 time steps, which was long enough to reach the ecological equilibrium in all non-evolutionary scenarios, and 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 its 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.

**Results**

*Comparison 1:* Reducing heritability to zero effectively eliminates evolution by natural selection, revealing how trait variation *per se* alters 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 time steps.

We also found that populations with stronger density dependence (i.e., higher values of *bs* and *ds*) experienced greater initial loss of trait variation (Figure 2, third row). This loss of variation slows the pace of evolution relative to the QG expectation. At intermediate and low density dependence, the initial loss of trait variation was only 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 2, left column). However, all populations displayed considerable individual demographic stochasticity (Figure 2, bottom row), manifested as large differences in lifetime reproductive success among individuals with the same trait values. Intriguingly, however, the peaks in the observed lifetime reproductive success distributions were often considerably offset from the ESS.

To help understand this result, we calculated the expected lifetime reproductive success of an individual from the model:

The value of *bmax* that maximizes *R0* is given by the solution of the equation:

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 will change depending on the ecological conditions (i.e., the current population size). We term this transient peak on the fitness landscape a “transient evolutionary attractor” (TEA).

Re-examining the observed lifetime reproductive success values, you can see that the peak of the observed distribution is often centered on these TEAs (Fig. 2, bottom row), and that the observed evolutionary trajectory for *bmax* often appears to be approaching this TEA, rather than the ESS (Fig. 2, second row).

If we visualize the fitness landscape using lifetime reproductive succes, we can see how this landscape changes as the 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 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.