Classification**:** BIOLOGICAL SCIENCES: Evolution

**Transient evolutionary attractors alter evolutionary adaptation**

John P. DeLong\*1 and Clayton E. Cressler1

1School of Biological Sciences, University of Nebraska – Lincoln, Lincoln, NE, 68588, USA

\*Corresponding author

ORCID for JPD: 0000-0003-0558-8213

**ORCID for CEC:** 0000-0002-6281-2798

Keywords: stochastic dynamics, eco-evolutionary dynamics, GEM, Gillespie, maladaptation, harvest induced evolution

**Abstract**

The path toward adaptation is often visualized as a deterministic trajectory toward a fitness peak, but stochastic processes such as genetic drift may overwhelm selection and hinder adaptation. Moreover, ecological dynamics may move fitness peaks as the paths are followed, generating eco-evolutionary dynamics. Those dynamics may be subject to (sometimes strong) stochastic processes from demography and the environment. However, the effect of such stochasticity on evolution via its effect on ecological dynamics is poorly understood. Classic eco-evolutionary theory typically rests on the assumption of ecological equilibrium or a separation of evolutionary and ecological time scales, but here we relax these assumptions and 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 unexpected evolutionary outcomes. We also show, however, that these outcomes can be understood as being governed by transient evolutionary attractors (TEAs) that alter the path of evolution but that may not be visible through an equilibrium lens. We further show that harvesting that maintains populations in transient states can redirect evolution away from an ESS 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.

**Significance**

Understanding and predicting adaptive evolution requires understanding the map between traits and fitness. This mapping varies with ecological conditions, generating eco-evolutionary dynamics. Previous approaches to eco-evolutionary dynamics have focused on equilibrium conditions, but we show that fitness peaks may be predictably different during transient (non-equilibrium) periods. Our ability to predict the path of adaptation for threatened species, infectious diseases, harvested populations, or invasive species, all of which persist in non-equilibrium states, thus depends on a shift of evolutionary thinking toward non-equilibrium approaches.

**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 (1, 2) 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 (3, 4). Mathematical models have proven to be a valuable tool for studying the various ways that stochasticity can impact ecological (reviewed in (5, 6) and evolutionary (reviewed in (7) 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; (9, 10). Ecological theory has shown how stochasticity can excite an underlying deterministic tendency for a system to oscillate, leading to sustained oscillations (11, 12), and how it can cause systems to shift between different deterministic attractors (13, 14). However, despite this long-standing interest, there has been little work studying how stochasticity affects evolutionary dynamics *through* its effects on ecological dynamics.

Adaptation is often visualized with a fitness landscape where peaks represent locally optimal trait values, and where the “shape” of the landscape is determined by ecological interactions (2). Classical approaches to identifying such peaks typically start by assuming an ecological equilibrium and asking what traits maximize fitness at this equilibrium (15–17). This approach is fundamental to a wide range of theoretical work aimed at understanding the process of adaptation (18–21), and it is heuristically useful in that it allows visualization of adaptation as populations move toward a (possibly local) fitness maximum.

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 (22). In particular, the fitness landscape becomes dynamic, with peaks moving through trait space as ecological processes unfold. These feedbacks can be quite rapid, since the timescales of ecology and evolution are not as different as was once assumed (23–25). In a now-classic example, selection fluctuated between favoring grazing-resistant and rapidly growing algae genotypes due to cycles of grazing activity by rotifers (26). 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.

Given the key role of ecological dynamics in shaping fitness landscapes, stochasticity that alters ecological dynamics may also influence adaptation. At least two distinct kinds of stochasticity 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 both population size and the probability of fixation of beneficial alleles (27, 28). Environmental stochasticity is random variation in the environment that affects the vital rates of all individuals in a population. One often-overlooked form of environmental stochasticity present in all numerical analyses is the choice of initial conditions. The choice of initial conditions is set by the user and is therefore a kind of external, random force influencing population size, and the effect is to influence the transient dynamics of the system. For example, initial conditions can determine whether long transients arise in classic competition models or whether communities proceed more directly to an equilibrium (29). As such, transient dynamics generated by either demographic or environmental stochasticity could shape evolutionary dynamics by altering the ecological processes that give rise to the fitness landscape. Given that most populations experience such 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]; 30–32). Specifically, we compare the ecological and evolutionary dynamics produced by GEMs to deterministic expectations based on the quantitative genetics (QG) approach of Lande (16) and Abrams et al. (17). Demographic stochasticity is built into the structure of the GEMs through stochasticity in the birth and death process. Environmental stochasticity induced transient dynamics is introduced in two ways: 1) by varying the location of the ecological equilibrium (i.e., carrying capacity) but keeping the starting conditions the same, we vary the relative magnitude of the initial conditions effect, and 2) by introducing a cull to maintain populations below their equilibrium. We show that stochasticity often limit adaptation, preventing populations from reaching the expected evolutionary optimum, but find that, just as often, 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 we suggest that these TEAs may play an important role driving evolutionary dynamics in many natural systems. 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 (15, 16) 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 (17, 33–35), thus defining an eco-evolutionary model. The timescale of evolutionary change, relative to ecological change, depends on the amount of additive genetic (co)variance in the population (15). 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 (19, 21). 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 (19). Thus, typically, an eco-evolutionary 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.

To investigate whether transient behavior can influence 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 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 (average 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 of is an evolutionarily stable strategy (ESS) that maximizes fitness, and is equivalent to carrying capacity.

*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 (30–32). 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 (36, 37). 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 (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 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 (38–40). 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 (41). For example, Banks and Thompson (42) 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 in the damselfly population, 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 (7) or the loss of high-fitness genotypes (28).

*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, variance in *b*max will drive variance in *d*min. We therefore broke this apart to evaluate the effect of variance 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 variance altogether; by allowing variance in *b*max but holding *d*min constant; by allowing variance 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 whether in the absence of trait variance 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 (different levels of environmental stochasticity caused by the user). 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. We implemented a random cull to a specific abundance level below equilibrium. Thus, harvesting here 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, 0.04, and 0.005 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, 18.75, and 150 across the three scenarios; at the ESS value of *bmax*=5.4, the equilibrium abundances were 13.5, 33.75, and 270. 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 long enough to clearly identify its attractor, which was 50, 400, and 60 time steps for comparisons 1, 2, and 3 respectively. 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:* 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 *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 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, 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 3, 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 showed converge of the mean population trait () with the ESS trait value.

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 3, 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 3, left column). However, all populations displayed considerable individual demographic stochasticity (Figure 3, 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:

(Equation 4)

The value of *bmax* that maximizes *R0* 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, bottom row), and that the observed evolutionary trajectory for *bmax* often appears to be approaching this TEA, rather than the ESS (Fig. 3, second row).

If we visualize the fitness landscape using lifetime reproductive success, we can see how this landscape changes as the populations grew, generating TEAs that shifted along with the population (Figure 4). Populations moved along these fitness contours as the population grew toward its ecological equilibrium. Population trajectories, however, showed considerable stochastic variation in abundance 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 depended on the population size the cull produced (Figures 5,6). 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 6). 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 (16, 17, 22, 43–47). 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 that disrupts the abundance of populations 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 themselves change the ecological dynamics. In our case, by suppressing population sizes (Figure 2), 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, demographic and environmental 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 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 (18, 26, 48). Our results further this finding, demonstrating that even simple, single-species models can facilitate not just eco-evolutionary dynamics but generate 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 (49). 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 (50). 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.

**Acknowledgements**

This work was supported in part by a grant to JPD from James S. McDonnell Foundation Studying Complex Systems Scholar Award.

**References**

1. R. A. Fisher, *The Genetical Theory of Natural Selection: A Complete Variorum Edition* (OUP Oxford, 1930).

2. S. Wright, Evolution in Mendelian populations. *Genetics* **16**, 97–159 (1931).

3. H. G. Andrewartha, L. C. Birch, *The distribution and abundance of animals* (University of Chicago Press, 1954).

4. A. J. Nicholson, The self-adjustment of populations to change. *Cold Spring Harb Symp Quant Biol* **22**, 153–173 (1957).

5. T. Coulson, P. Rohani, M. Pascual, Skeletons, noise and population growth: the end of an old debate? *Trends Ecol. Evol. (Amst.)* **19**, 359–364 (2004).

6. A. J. Black, A. J. McKane, Stochastic formulation of ecological models and their applications. *Trends Ecol. Evol. (Amst.)* **27**, 337–345 (2012).

7. T. Lenormand, D. Roze, F. Rousset, Stochasticity in evolution. *Trends in Ecology & Evolution* **24**, 157–165 (2009).

8. J. A. Coyne, N. H. Barton, M. Turelli, Perspective: A Critique of Sewall Wright’s Shifting Balance Theory of Evolution. *Evolution* **51**, 643–671 (1997).

9. D. Cohen, Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* **12**, 119–129 (1966).

10. D. Z. Childs, C. J. E. Metcalf, M. Rees, Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proc. Biol. Sci.* **277**, 3055–3064 (2010).

11. J. V. Greenman, T. G. Benton, The amplification of environmental noise in population models: causes and consequences. *Am. Nat.* **161**, 225–239 (2003).

12. A. J. McKane, T. J. Newman, Predator-prey cycles from resonant amplification of demographic stochasticity. *Phys. Rev. Lett.* **94**, 218102 (2005).

13. S. M. Henson, J. M. Cushing, R. F. Costantino, B. Dennis, R. A. Desharnais, Phase switching in population cycles. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**, 2229–2234 (1998).

14. P. Ashwin, S. Wieczorek, R. Vitolo, P. Cox, Tipping points in open systems: bifurcation, noise-induced and rate-dependent examples in the climate system. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **370**, 1166–1184 (2012).

15. R. Lande, Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**, 314–334 (1976).

16. R. Lande, A quantitative genetic theory of Life history evolution. *Ecology* **63**, 607–615 (1982).

17. P. A. Abrams, Y. Harada, H. Matsuda, On the relationship between quantitative genetic and ESS models. *Evolution* **47**, 982–985 (1993).

18. G. F. Fussmann, S. P. Ellner, N. G. Hairston Jr, Evolution as a critical component of plankton dynamics. *Proc. Biol. Sci.* **270**, 1015–1022 (2003).

19. M. H. Cortez, S. P. Ellner, Understanding rapid evolution in predator‐prey interactions using the theory of fast‐slow dynamical systems. *Am. Nat.* **176**, E109-127 (2010).

20. D. A. Vasseur, P. Amarasekare, V. H. W. Rudolf, J. M. Levine, Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. *Am. Nat.* **178**, E96–E109 (2011).

21. M. H. Cortez, How the magnitude of prey genetic variation alters predator-prey eco-evolutionary dynamics. *The American Naturalist* **188**, 329–341 (2016).

22. L. Govaert, *et al.*, Eco-evolutionary feedbacks—Theoretical models and perspectives. *Functional Ecology* **33**, 13–30 (2019).

23. N. G. Hairston, Jr., S. P. Ellner, M. A. Geber, T. Yoshida, J. A. Fox, Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.* **8**, 1114–1127 (2005).

24. T. W. Schoener, The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* **331**, 426–429 (2011).

25. J. P. DeLong, *et al.*, How fast is fast? Eco-evolutionary dynamics and rates of change in populations and phenotypes. *Ecol Evol* **6**, 573–581 (2016).

26. T. Yoshida, L. E. Jones, S. P. Ellner, G. F. Fussmann, N. G. Hairston, Jr., Rapid evolution drives ecological dynamics in a predator-prey system. *Nature* **424**, 303–306 (2003).

27. J. B. S. Haldane, The cost of natural selection. *J. Gen.* **55**, 511–524 (1957).

28. B. J. Crespi, The evolution of maladaptation. *Heredity (Edinb)* **84 ( Pt 6)**, 623–629 (2000).

29. A. Hastings, Transients: the key to long-term ecological understanding? *Trends Ecol. Evol. (Amst.)* **19**, 39–45 (2004).

30. J. P. DeLong, J. P. Gibert, Gillespie eco-evolutionary models (GEMs) reveal the role of heritable trait variation in eco-evolutionary dynamics. *Ecol Evol* **6**, 935–945 (2016).

31. J. P. DeLong, T. M. Luhring, Size-dependent predation and correlated life history traits alter eco-evolutionary dynamics and selection for faster individual growth. *Popul Ecol* **60**, 9–20 (2018).

32. J. P. DeLong, J. Belmaker, Ecological pleiotropy and indirect effects alter the potential for evolutionary rescue. *Evolutionary Applications* **12**, 636–654 (2019).

33. M. L. Taper, T. J. Case, Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* **46**, 317–333 (1992).

34. P. A. Abrams, H. Matsuda, Y. Harada, Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol Ecol* **7**, 465–487 (1993).

35. P. A. Abrams, H. Matsuda, Prey adaptation as a cause of predator-prey cycles. *Evolution* **51**, 1742–1750 (1997).

36. D. T. Gillespie, Exact stochastic simulation of coupled chemical reactions. *J. Phys. Chem.* **81**, 2340–2361 (1977).

37. G. Yaari, Y. Ben-Zion, N. M. Shnerb, D. A. Vasseur, Consistent scaling of persistence time in metapopulations. *Ecology* **93**, 1214–1227 (2012).

38. B. E. Kendall, G. A. Fox, M. Fujiwara, T. M. Nogeire, Demographic heterogeneity, cohort selection, and population growth. *Ecology* **92**, 1985–1993 (2011).

39. J. P. Stover, B. E. Kendall, G. A. Fox, Demographic heterogeneity impacts density-dependent population dynamics. *Theor Ecol* **5**, 297–309 (2012).

40. C. E. Cressler, S. Bengtson, W. A. Nelson, Unexpected nongenetic individual heterogeneity and trait covariance in *Daphnia* and its consequences for ecological and evolutionary dynamics. *The American Naturalist* **190**, E13–E27 (2017).

41. S. F. van Daalen, H. Caswell, Lifetime reproductive output: individual stochasticity, variance, and sensitivity analysis. *Theor Ecol* **10**, 355–374 (2017).

42. M. J. Banks, D. J. Thompson, Lifetime reproductive success of females of the damselfly *Coenagrion puella*. *Journal of Animal Ecology* **56**, 815–832 (1987).

43. D. L. DeAngelis, W. M. Mooij, Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics* **36**, 147–168 (2005).

44. T. Coulson, T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, Putting evolutionary biology back in the ecological theatre: a demographic framework mapping genes to communities. *Evol Ecol Res* **8**, 1155–1171 (2006).

45. S. P. Ellner, M. Rees, Integral projection models for species with complex demography. *Am. Nat.* **167**, 410–428 (2006).

46. S. Lion, Theoretical approaches in evolutionary ecology: Environmental feedback as a unifying perspective. *The American Naturalist* **191**, 21–44 (2017).

47. C. de Vries, H. Caswell, Stage-structured evolutionary demography: Linking life histories, population genetics, and ecological dynamics. *The American Naturalist* **193**, 545–559 (2019).

48. M. H. Cortez, J. S. Weitz, Coevolution can reverse predator–prey cycles. *Proc Natl Acad Sci U S A* **111**, 7486–7491 (2014).

49. C. T. Darimont, *et al.*, Human predators outpace other agents of trait change in the wild. *PNAS* **106**, 952–954 (2009).

50. E. Edeline, *et al.*, Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *PNAS* **104**, 15799–15804 (2007).

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* (42). 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 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.

Figure 3. 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 (0.1, 0.04, 0.005). The median and middle 50% of GEM trajectories 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.

Figure 4. 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.

Figure 5. 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.

Figure 6. 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).

Figure 1.

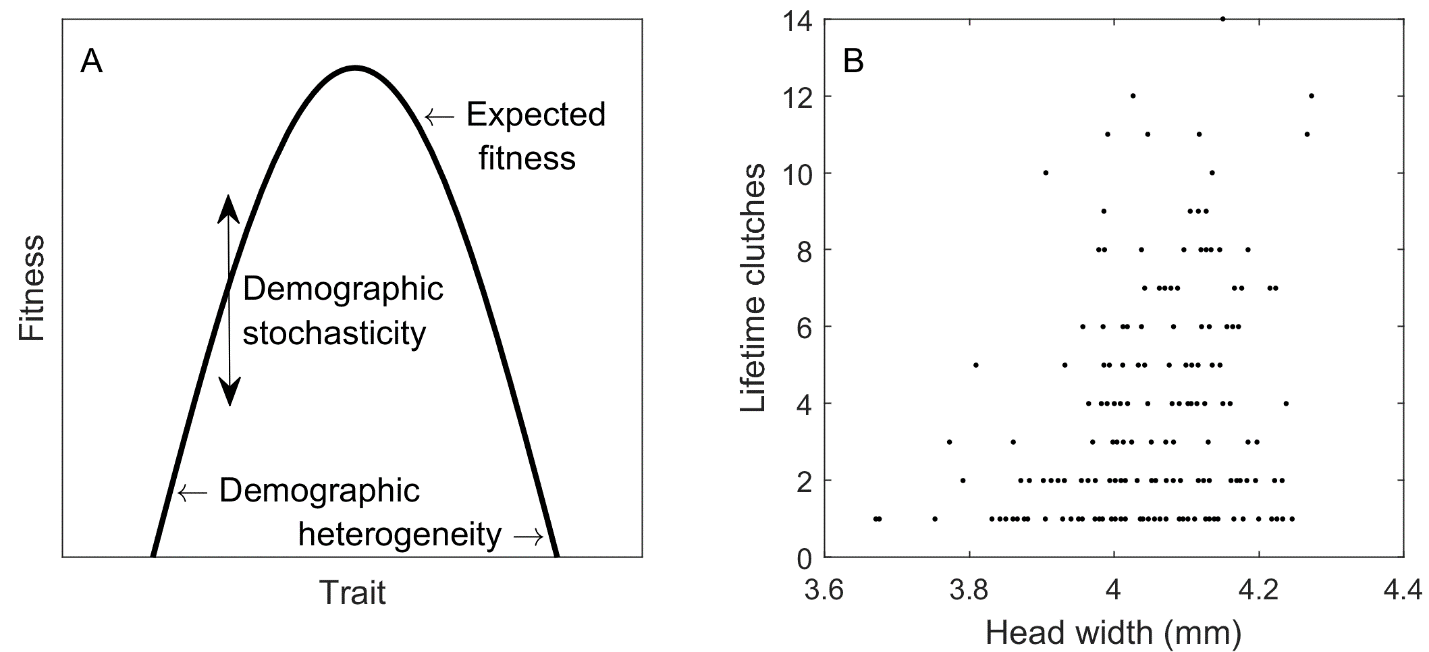


Figure 2.

C:\Users\jdelong2\AppData\Local\Microsoft\Windows\INetCache\Content.Word\Figure 2 effect of variance.tif

Figure 3.

C:\Users\jdelong2\AppData\Local\Microsoft\Windows\INetCache\Content.Word\Figure 3 vary K dynamics_long.tif

Figure 4.

C:\Users\jdelong2\AppData\Local\Microsoft\Windows\INetCache\Content.Word\Figure 3 vary K landscape_long.tif

Figure 5.

C:\Users\jdelong2\AppData\Local\Microsoft\Windows\INetCache\Content.Word\Figure 5 cull from ESS dynamics.tif

Figure 6.

C:\Users\jdelong2\AppData\Local\Microsoft\Windows\INetCache\Content.Word\Figure 6 vary cull from ESS fitness landscape.tif