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## ARTICLE

# Stochasticity directs adaptive evolution toward nonequilibrium evolutionary attractors

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**Abstract**

Stochastic processes such as genetic drift may 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 variation in 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 are governed by nonequilibrium evolutionary attractors—these are maxima in lifetime reproductive success when stochasticity keeps the ecological system away from the deterministic equilibrium. These NEEAs alter the path of evolution but are not visible through the equilibrium lens that underlies much evolutionary theory. Our results reveal that considering population processes during transient periods can greatly improve our understanding of the path and pace of evolution.

**KEYWORDS**

eco-evolutionary dynamics, Gillespie eco-evolutionary model, Gillespie algorithm, maladaptation, stochastic dynamics

## INTRODUCTION

At the most fundamental level, ecological and evolutionary dynamics result from the individual-level stochastic processes of birth, death, and mutation. In a large enough population, the stochasticity of these processes is relatively unimportant, and as a result, mathematical theory in both ecology and evolutionary biology has tended to assume that deterministic population-level dynamical models are sufficient to describe ecological and evolutionary dynamics and outcomes. Indeed, existing evolutionary theories, such as the “canonical equation of adaptive dynamics,” can be derived as limiting cases of a general stochastic model (e.g., large population sizes with rare mutations of small effect: [Champagnat et al., 2006;

Costa et al., 2016; Dieckmann & Law, 1996]), supporting their value as general tools for studying ecology and evolution. These deterministic models have therefore become the basis for numerous advances in our understanding of eco-evolutionary dynamics (Cortez & Weitz, 2014; Fussmann et al., 2003; Govaert et al., 2019; Tirok et al., 2011; Vasseur et al., 2011; Yoshida et al., 2004).

Many populations, however, show substantial stochasticity in their ecological dynamics, even when the populations are not particularly small (Lande et al., 2003; Nisbet & Gurney, 2004; Shoemaker et al., 2020). This stochasticity has been shown to substantially alter evolutionary predictions. The effects can be straightforward, such as the direct effect of genetic drift in slowing adaptation and causing the loss of high-fitness genotypes

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(Lande, 1976). Other effects include reversals of expectations from the deterministic expectations. For example, demographic stochasticity can favor the evolution of slower-growing strategies if they have lower variance in reproduction (e.g., bet hedging; Gillespie, 1975; Parsons et al., 2018), even though the deterministic expectation is for faster-growing strategies to evolve. Similarly, stochasticity can favor cooperative strategies that improve the environment for everyone (e.g., altruism; Constable et al., 2016), in contrast to the deterministic expectation that altruistic populations are easily invaded by “cheaters” that benefit from public goods production without reciprocating (the “tragedy of the commons”). These studies suggest that a deeper understanding of the impact of stochasticity on eco-evolutionary dynamics is critically needed.

A fundamental component of deterministic eco-evolutionary models is the evolutionarily stable strategy (ESS) (Smith & Price, 1973). An ESS arises given trade-offs among traits that contribute to fitness, such that there is one combination of traits that maximizes fitness (locally) and cannot be invaded by individuals with nearby trait combinations. In the preceding examples, trade-offs occur between transmission and virulence (Parsons et al., 2018), growth rate and variance in growth (Gillespie, 1975), and the costs and benefits of public goods production (Constable et al., 2016). There are many trade-offs among life history traits, however, that may influence evolutionary dynamics and, thus, many possible ways in which an ESS may arise in deterministic models. A commonly considered trade-off is that between reproduction and mortality (Reznick et al., 2000; Stearns, 1976). This trade-off has been widely demonstrated across plants, invertebrates, and vertebrates (Lee et al., 2008; Wilder et al., 2013), and its existence suggests there should be an evolutionarily stable combination of birth rate and survival that maximizes fitness at a population’s carrying capacity. But the effect of stochasticity on such an ESS is unknown, despite its centrality to life history theory and its connection to a wide range of eco-evolutionary modeling efforts (e.g., Cortez & Weitz, 2014; Fussmann et al., 2003; Tirok et al., 2011).

Here we use Gillespie eco-evolutionary models (GEMs) (DeLong & Gibert, 2016; DeLong & Luhning, 2018) to generate ecological and evolutionary dynamics through the simulation of stochastic birth–death processes (Champagnat et al., 2006; Dieckmann & Law, 1996; Doebeli et al., 2017). Specifically, we test the hypothesis that stochasticity will alter the expected evolutionary outcomes by guiding trait evolution to a location other than that predicted by the ESS. We compare dynamics from our GEMs given an underlying trade-off between births and deaths to deterministic expectations using a quantitative genetics (QG) approach (Abrams et al., 1993; Lande, 1976).

We show that when demographic stochasticity causes the asymptotic population size to be different than the deterministic expectation, the birth trait evolves toward a different attractor that maximizes lifetime reproductive success (LRS), rather than maximizing per-capita growth rate as assumed in the deterministic approach. We term this alternative attractor a nonequilibrium evolutionary attractor (NEEA), as stochasticity prevents the population dynamics from reaching the expected equilibrium. In combination with previous work (Gillespie, 1975; Parsons et al., 2018), we suggest that these NEEAs may arise in numerous ways and play an important role in driving evolutionary dynamics in many natural systems and, more generally, that understanding transient eco-evolutionary phenomenon may provide new insights into how populations evolve.

## MATERIAL AND METHODS

### Deterministic eco-evolutionary dynamics

The QG 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 QG equations of Lande (1976), which assume that the trait distribution is unimodal and that the variance in fitness is greater than the variance in the trait (Abrams et al., 1993; Abrams, 2001). An identical expression can also be derived from the dynamics of genotypes via the Price equation (Taylor & Day, 1997). 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., 1993; Taylor & Day, 1997; Tirok et al., 2011).

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

$$\frac{dR}{dt} = (b_{\max} - b_s R)R - (d_{\min} + d_s R)R, \quad (1)$$

where  $R$  is population abundance,  $b_{\max}$  is the maximum birth rate,  $d_{\min}$  is the minimum death rate, and  $b_s$  and  $d_s$  characterize the effects of population abundance on the realized birth and death rates, respectively. This model is a simple expansion of the logistic model (DeLong & Coblenz, 2022), with the maximum rate of population growth given as  $r_{\max} = b_{\max} - d_{\min}$  and a carrying capacity defined as  $K = \frac{b_{\max} - d_{\min}}{b_s + d_s}$ . We redefine the logistic model this way to allow us to simulate the ecological

dynamics as a stochastic birth–death process rather than a process with a net rate of population growth (Doebeli et al., 2017). We chose 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; Lee et al., 2018).

We consider the case where the maximum birth rate ( $b_{\max}$ ) is evolving and is connected to the minimum mortality rate through a classic life-history trade-off between reproduction and mortality (i.e., the minimum death rate  $d_{\min}$  is a function of  $b_{\max}$ ) (Reznick et al., 2000; Stearns, 1976). More practically, positing such a trade-off facilitates our analysis because it leads to an evolutionary equilibrium where fitness (here, the per-capita rate of population growth) is maximized. Using the QG approach, the dynamics of the population mean trait,  $\overline{b_{\max}}$ , are given by  $\frac{d\overline{b_{\max}}}{dt} = V \left( \frac{\partial W}{\partial b_{\max}} \right)_{b_{\max}=\overline{b_{\max}}}$ , where  $V$  is the additive genetic variance (or the product of phenotypic variance and narrow-sense heritability) in  $b_{\max}$ ,  $W = \frac{1}{R} \left( \frac{dR}{dt} \right)$  is the per-capita growth rate given the trait (i.e., mean individual fitness), and  $\left( \frac{\partial W}{\partial b_{\max}} \right)_{b_{\max}=\overline{b_{\max}}}$  is the fitness gradient evaluated at the mean trait. The fitness gradient will vanish at any potential evolutionary equilibrium. Given the preceding Equation (1), the fitness gradient is equal to  $1 - d'_{\min}(\overline{b_{\max}})$ , which implies that the minimum death rate ( $d_{\min}$ ) must be an increasing function of the maximum birth rate ( $b_{\max}$ ) for an evolutionary equilibrium to exist (otherwise the fitness gradient will not change sign). For any equilibrium to represent a fitness maximum requires  $\frac{\partial^2 W}{\partial b_{\max}^2} = -d''_{\min}(b_{\max}) < 0$ , which implies that the minimum death rate ( $d_{\min}$ ) must be an accelerating function of maximum birth rate ( $b_{\max}$ ). As such, we assume that  $d_{\min} = cb_{\max}^2$ , where  $c$  is a trade-off constant, making the equation for the evolutionary dynamics

$$\frac{d\overline{b_{\max}}}{dt} = V(1 - 2c\overline{b_{\max}}) \quad (2)$$

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

$$\left( \hat{R} = K = \frac{\overline{b_{\max}} - \overline{d_{\min}}}{b_s + d_s}, \overline{b_{\max}} = \frac{1}{2c} \right). \quad (3)$$

We call this value of the mean maximum birth rate ( $\overline{b_{\max}}$ ) an ESS since it is an evolutionary equilibrium where other trait values cannot invade and where fitness is maximized.

## Stochastic eco-evolutionary dynamics

GEMs simulate ecological dynamics through a stochastic birth-death process (DeLong & Gibert, 2016; DeLong & Luhning, 2018) and build on the standard Gillespie algorithm for simulating ODE models, which allows demographic stochasticity (random variation in the sequence and number of demographic events) to influence population outcomes (Gillespie, 1977). By incorporating demographic heterogeneity (variation among individuals in expected demographic traits) into the population and allowing the heritability of traits between parents of offspring, evolutionary dynamics emerge from the sequence of births and deaths. Unlike with a standard Gillespie algorithm, where population size is represented by a number, in a GEM, populations are represented as a collection of individuals with distinct trait values (e.g., parameters of the ecological model). Upon initiation of the simulation, the traits of these individuals are drawn from a probability distribution with a predefined mean and variance, with the type of distribution depending on the nature of the trait. Here, the trait of interest is maximum birth rate ( $b_{\max}$ ), which also determines the minimum death rate ( $d_{\min}$ ) through the trade-off function. Since  $b_{\max}$  can only take positive values, we draw the  $b_{\max}$  values for the initial population from a lognormal distribution.

In a GEM, an individual's trait value determines its probability of giving birth or dying. At each time step, an individual is chosen at random and its probability of birth or death is calculated by dividing the respective rate term by the sum of all rate terms. Because events generally do not have the same probability of occurrence, which event occurs is determined by a random draw from a uniform distribution (e.g., if the probability of birth is 0.4 and the probability of death is 0.6, the individual gives birth if the random draw is between 0 and 0.4 and dies otherwise). If the event is a death, that individual (really its trait) is removed from the population. If the event is a birth, a new individual is added to the population, and its trait ( $b_{\max}$ ) is drawn from a lognormal distribution with a mean and variance that are determined by the parental trait and specified rules for heritability of that trait (Appendix S1). As a GEM is running, the loss and addition of individuals in the population affect both population dynamics and the dynamics of both the mean and variance of the trait distribution(s). Populations gradually lose individuals with a high likelihood of mortality and gradually add individuals with a higher likelihood of births, generating natural selection without needing to specify fitness gradients, explicit equations for the trait dynamics, or the expected trait equilibria such as an ESS. Evolutionary dynamics thus emerge out of the stochastic

births and deaths of individuals within the population (Champagnat et al., 2006; Dieckmann & Law, 1996; Doebeli et al., 2017), even as they are built on the deterministic equations that can be used to formulate QG and AD approaches (Luhning & DeLong, 2020).

We evaluated differences between the GEM and QG approaches by comparing outcomes across three different levels of density dependence. We set the initial carrying capacity ( $K$ ) at 10, 20, and 40 individuals, created by setting  $b_s = d_s = 0.075, 0.0375, \text{ and } 0.01875$ , respectively; note that as the populations evolve and  $\overline{b_{\max}}$  changes, the carrying capacity changes as well (Equation 3). We initialized populations with five individuals; in this first set of simulations, each individual's trait was drawn from a distribution with a mean that was below the ESS ( $\overline{b_{\max}} = 2$ ); later we will consider simulations where the mean of the distribution started above the ESS. The ESS  $\overline{b_{\max}}$  for this system is 5.4, which means the ESS  $\overline{d_{\min}}$  is 2.7. The CV of the evolving trait (maximum birth rate,  $b_{\max}$ ) in the initial population was 0.3, such that the mean initial variance in  $b_{\max}$  was about 0.29 (due to stochastic sampling), and heritability ( $h^2$ ) was 0.75. For a check on the effect of the trade-off parameter, we also varied  $c$  (values of 0.06, 0.09, and 1.2) using the same trait values and one level of density dependence ( $b_s = d_s = 0.04$ ). We expected that populations with a smaller carrying capacity would demonstrate greater stochasticity and average abundances farther below their expected carrying capacity than in the populations with larger carrying capacities, generating a more pronounced effect of nonequilibrium asymptotic behavior on the evolving trait. We expected a higher carrying capacity—and thus lower stochasticity—to facilitate convergence of the GEM solution with the QG solution. We ran each simulation for 400 time steps and replicated each stochastic simulation 50 times. All simulations and ODE solutions were implemented in Matlab version 2021a, and code is available at Zenodo (DeLong, 2022). Abundances and traits of populations that went extinct were included in the results while they were extant. The number of extinctions that occurred was 39, 4, and 0 extinctions in runs with  $K = 10, 20, \text{ and } 40$ , respectively. Because extinct populations do not have traits, they could not be included after extinction and were thus not included for either traits or abundances.

To evaluate patterns in individual fitness (here, LRS) 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 maximum birth rate ( $b_{\max}$ ) and LRS. We do this for the population toward the end of the simulation (born after time step 350), including only individuals that died before the end of the simulation.

## RESULTS

We found that all populations grew toward the expected ecological equilibrium and that  $b_{\max}$  evolved toward the ESS across all levels of density dependence (Figure 1, first, second, and fifth rows). Although no population was able to grow or evolve as fast as expected from QG (Figure 1, first and second rows), the population experiencing the least density dependence converged to the expected eco-evolutionary equilibrium, whereas the populations with higher density dependence (and, hence, smaller deterministic equilibrium population sizes) lagged behind. The depiction of the eco-evolutionary dynamics in the phase plane (Figure 1, fifth row) is also illustrative: the initial ecological dynamics are much faster than the evolutionary dynamics (i.e., 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 toward the eco-evolutionary equilibrium given by the orange point (Figure 1, fifth row).

Nonevolutionary versions of our models (i.e.,  $h^2 = 0$ ) with no trait variation indicate that demographic stochasticity per se is part of the reason that abundances may not reach the carrying capacity (Appendix S2: Figure S1; Lande et al., 2003; Nisbet & Gurney, 2004). Adding trait variation can further suppress abundances, with the magnitude of that effect dependent on which traits have variation (Appendix S2: Figure S1). 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 1, left column). However, all populations displayed considerable individual demographic stochasticity (Figure 1, fourth row), manifested as large differences in LRS among individuals with the same trait values (van Daalen & Caswell, 2017). In addition, there was considerable demographic heterogeneity in the populations even after the distribution of maximum birth rate ( $b_{\max}$ ) values had centered on the optimal (ESS) values.

It is also clear that the evolutionary dynamics often do not reach the expected deterministic evolutionary equilibrium, especially in small populations where demographic stochasticity is strong. In particular, the median of the stochastic trajectories often settles onto or approaches a trait value that is noticeably smaller than the ESS (Figure 1, second and fifth rows). To help understand this result, we calculated the expected LRS of an individual (over time in their life,  $\tau$ ) from the model as follows:



$$\text{LRS} = \int_{t_b}^{\infty} (b_{\max} - b_s R(t)) e^{-\int_{t_b}^t (d_{\min} + d_s R(\tau)) d\tau} dt. \quad (4)$$

If  $R(t)$  reaches an equilibrium,  $R(t) = \hat{R}$ , then these integrals simplify, and LRS is the ratio of the per-capita birth and death rates,  $\text{LRS} = (b_{\max} - b_s \hat{R}) / (d_{\min} + d_s \hat{R})$ .

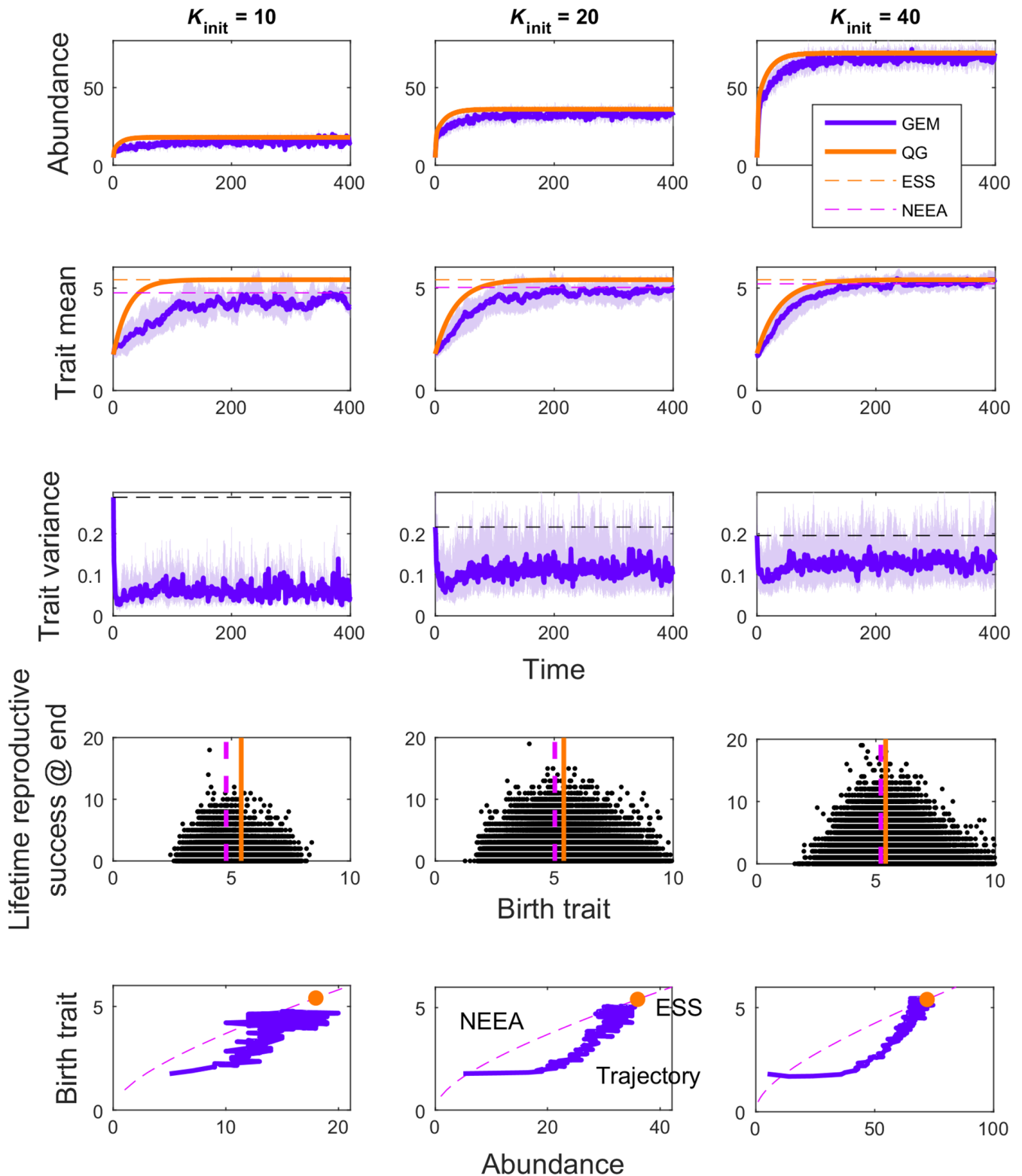


FIGURE 1 Legend on next page.

At such an equilibrium, the value of maximum birth rate ( $b_{\max}$ ) that maximizes LRS is given as follows by the solution of the equation  $\frac{\partial \text{LRS}}{\partial b_{\max}} = 0$ :

$$b_{\max} = b_s R + \sqrt{(b_s R)^2 + \frac{d_s R}{c}}. \quad (5)$$

This deterministic LRS (a NEEA) provides an alternative fitness metric that we can compare to the stochastically realized LRS in our GEM simulation. Note that the value of  $b_{\max}$  that maximizes the expected LRS is not necessarily the same as the ESS value (although when  $R$  is at its deterministic equilibrium, the values are the same). It is particularly important that this value depends on the current population size, meaning that the value of  $b_{\max}$  that maximizes LRS changes as the population grows. Examination of the observed LRS values from our simulations reveals that the peak of the LRS distribution occurs at the  $b_{\max}$  value that maximizes LRS (i.e., the NEEA; Figure 1, fourth row) and that the observed evolutionary trajectory for  $b_{\max}$  often appears to be approaching this LRS peak rather than the ESS (Figure 1, second and fifth rows). The outcome in which populations evolved toward the LRS peak rather than an ESS holds across a range of values for the trade-off slope,  $c$  (Appendix S3: Figure S1).

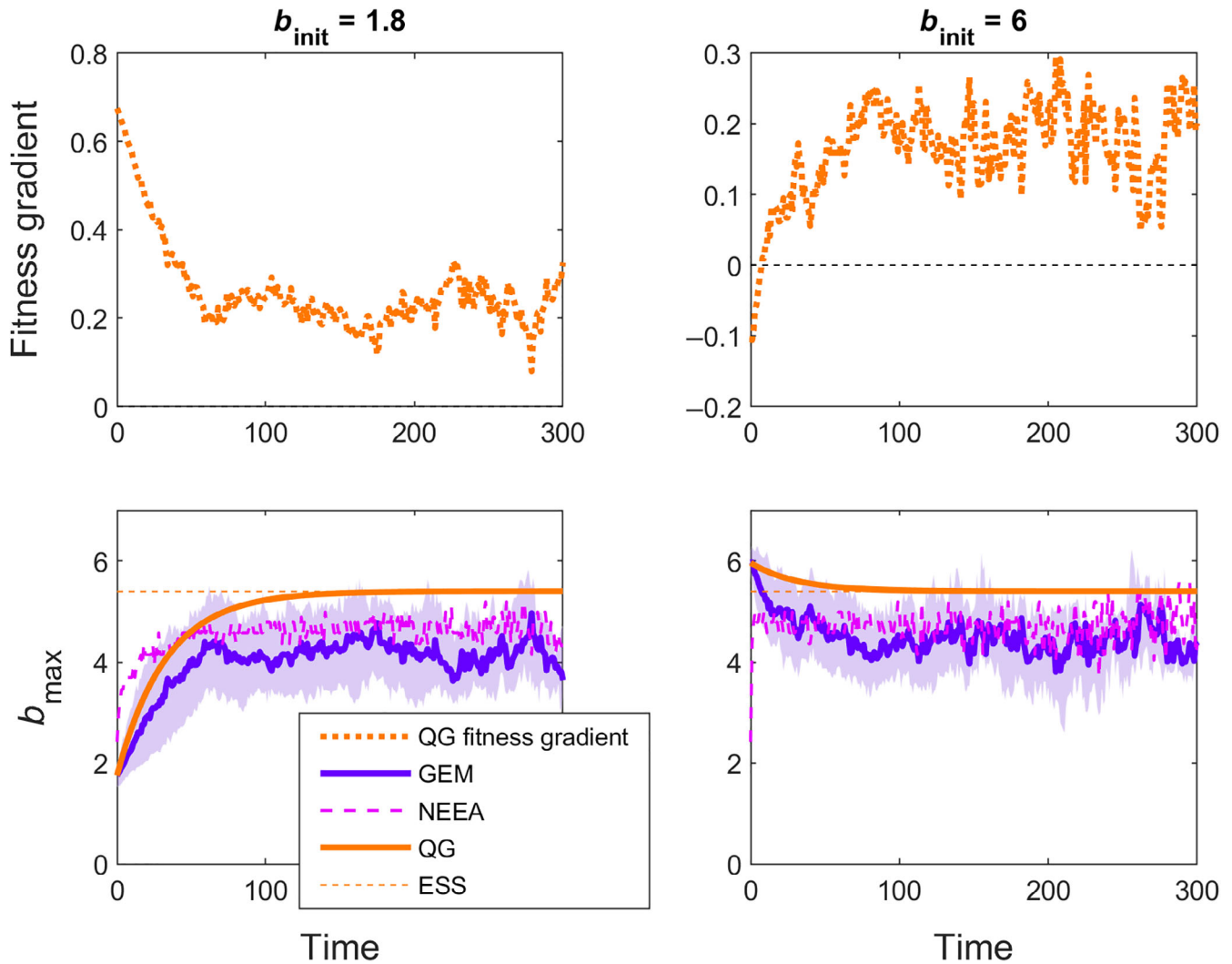
However, because the LRS peak occurred below the ESS and we initiated populations with a mean  $b_{\max}$  below the ESS, there is a possibility that trait evolution did not reach the ESS because it was constrained by genetic drift. That is, as the trait approaches the ESS, the fitness gradient becomes shallower, selection against mildly maladapted individuals weakens, and genetic drift can prevent the trait mean from getting closer to the ESS. This is the evolutionary analog of how demographic stochasticity prevents the population size from reaching the expected ecological equilibrium. In other words, we may have observed the outcome of selection–drift balance rather than evolution toward an alternative fitness peak. Alternatively, the failure to reach the expected evolutionary equilibrium could have

been caused by a loss of genetic variability needed to drive adaptive evolution. Indeed, populations with stronger density dependence (i.e., higher values of  $b_s$  and  $d_s$  and, therefore, lower  $K_{\text{init}}$  values) experienced greater initial loss of trait variation (Figure 1, third row), which further slowed the pace of evolution relative to the QG expectation. To evaluate these possibilities, we reran our high-density-dependent simulation with the mean  $b_{\max}$  initiated above the ESS. If our results were due to selection–drift balance, we would have expected the trait mean to equilibrate slightly above the ESS, once selection had weakened. Instead, we observed  $b_{\max}$  decline past the ESS toward the LRS peak, given the asymptotic population size (Figure 2).

## DISCUSSION

Ecological and evolutionary theory leans heavily on the assumption of an ecological equilibrium in both the derivation of approaches and predictions about the path and outcomes of evolution (Abrams et al., 1993; Lande, 1976). In particular, almost all derivations of ESSs, combinations of traits that maximize fitness and cannot be invaded by other nearby strategies, assume that the ecological dynamics are equilibrational (but see Hite & Cressler, 2018; Hoyle et al., 2011; Metz et al., 1992). The identification—and mere existence—of an ESS guides our intuition about evolution and the dynamics leading to particular ecological and evolutionary outcomes. But the assumption of ecological equilibrium will often be violated in many systems in nature, given that many systems may be dynamically tracking environmental change or recovering from perturbations. Furthermore, demographic stochasticity can alter ecological dynamics and reduce the ability of even unperturbed systems from reaching an ecological equilibrium (Lande et al., 2003; Nisbet & Gurney, 2004). Indeed, much of the ecological and evolutionary patterns we can observe may be nonequilibrium, and as a result, the effect of demographic stochasticity—and transient dynamics more generally

**FIGURE 1** Gillespie eco-evolutionary model (GEM) simulations of birth–death logistic model. The rows show from top to bottom population abundance, mean maximum birth rate ( $b_{\max}$ ), 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  $b_{\max}$  remains 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 evolutionarily stable strategy (ESS) and the nonequilibrium evolutionary attractors (NEEAs) 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 50 time steps. The evidence that the population evolves toward the NEEA 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. The dashed black line in row three is the average initial trait variance in the population.



**FIGURE 2** Gillespie eco-evolutionary model (GEM) simulations of birth–death logistic model. The fitness gradient for mean maximum birth rate ( $b_{max}$ ) is in the upper row, and  $b_{max}$  is in the second row. The columns differ in the initial starting value of  $b_{max}$ . Colors are the same as in Figure 1, with bold orange showing quantitative genetics (QG) outcomes, dashed orange showing the evolutionary stable strategy (ESS), pink showing the nonequilibrium evolutionary attractor (NEEA), and purple the GEM outcome. The fact that in both scenarios the trait evolves to below the ESS and toward the NEEA indicates that the outcome is driven not by a shifting balance between genetic drift and selection but by the peak in lifetime reproductive success that occurs away from the ESS during transient, nonequilibrium conditions.

(Hastings et al., 2018)—is of critical importance to our understanding of ecological and evolutionary patterns.

Our results show that whenever stochasticity is strong enough to alter the ecological steady state, the evolutionary outcome of the commonly invoked and observed trade-off between reproduction and mortality is different from that predicted by classical deterministic theory (Figure 1). This result suggests that a stochastic view of evolutionary dynamics will be critical whenever attempting to understand evolution in rare or invading populations or populations subject to perturbations or fluctuating environmental conditions. Together with previous work demonstrating the effect of stochasticity on the evolution of other traits, our work points to the

existence of another class of attractors—NEEAs. Critically, these attractors are not necessarily fixed in time. They may approach a relatively constant value if the deterministic ecological system is expected to reach an equilibrium (although stochasticity can still sometimes excite an underlying tendency to oscillate [McKane & Newman, 2005]), but while the population is growing or decaying, the optimal value will be changing too, causing the system to chase the attractor (Figure 1), converging with the ESS only if and when the population reaches the expected ecological equilibrium (e.g., its carrying capacity).

Our results also contribute to the body of theory exploring the connection between “macroscopic” models



of trait evolution (e.g., equations for the dynamics of the population mean traits) and the underlying “microscopic” stochastic processes of individual birth, death, and mutation (Doebeli et al., 2017). Other authors have revealed how many of the classic “macroscopic” models of evolutionary theory can be derived as limiting cases of stochastic individual-level birth–death–mutation processes. For example, in a landmark series of papers (Champagnat, 2006; Champagnat et al., 2001, 2006), Champagnat and colleagues showed that, from a general stochastic model of births, deaths, and mutation, one can derive the “continuum-of-alleles” model of population genetics (Crow & Kimura, 1965; Kimura, 1965) by assuming a large population size; by adding the assumptions of rare mutations of small effect, one recovers the canonical equation of adaptive dynamics (Dieckmann & Law, 1996). The rigorous approach described in these papers has been extended to consider other evolutionary scenarios, such as the coevolution of predators and prey (Costa et al., 2016), showing again that classic eco-evolutionary models can be recovered under appropriate assumptions. Other authors have considered special cases where, for example, the assumption of large population size is relaxed, but these approaches often consider only a limited number of interacting types (Constable et al., 2016; Parsons et al., 2010; Parsons & Quince, 2007); for example, if evolution is mutation limited but population sizes are finite, Parsons et al. was able to derive a “stochastic adaptive dynamics” model that recapitulates classic AD predictions when population size is large (Parsons et al., 2018).

However, at the moment, there is still no general theory that can be derived from stochastic birth–death–mutation processes that can deal with the biologically realistic situation where population sizes are finite and ecological and evolutionary processes happen on similar timescales (i.e., mutations are neither particularly rare nor of small effect). The impression this gives is that it is challenging to describe stochastic eco-evolutionary dynamics with accessible mathematics, but this may not always be the case. Although the model we investigate is relatively simple, our results suggest that we can look to LRS as a flexible indicator of evolutionary expectations in nonequilibrium systems. Both our expressions for LRS (Equations 4 and 5) contain  $R$  (population abundance), indicating that we can predict the trait with the highest fitness at any moment as population size changes. Indeed, our results show clear changes in the optimal trait, with trait evolution chasing this optimal trait through time. It thus may be possible, even in complex models, to make nonequilibrium predictions for the path and outcome of evolution, including the identification of NEEAs that might mimic ESSs whenever a nonequilibrium steady state ensues.

This means that the deterministic models may still provide useful insights, even when stochasticity is important, because they contain the terms needed to estimate LRS. Several authors have shown that, in a finite population, the probability of fixation of a mutant allele is a better predictor of evolutionary dynamics than the canonical equation of adaptive dynamics (Champagnat & Lambert, 2007; Débarre & Otto, 2016; Proulx & Day, 2001). The probability of fixation for an allele (trait)  $a$  is  $1 - \frac{d(a)}{b(a)}$  (Champagnat, 2006; Dieckmann & Law, 1996; Proulx & Day, 2001), which is equivalent to  $1 - 1/\text{LRS}$ . These models derive this result by considering competition between two populations with distinct alleles (Parsons & Quince, 2007). Here, we show that LRS predicts the evolutionary outcome when populations are composed of individuals each of whom has a unique trait and where mutations are neither rare nor small. Finally, our approach to simulating evolution via a simple extension of the familiar Gillespie algorithm provides an accessible entry point for studying eco-evolutionary dynamics to ecologists who are comfortable with deterministic ecological models (DeLong & Coblenz, 2022; DeLong & Gibert, 2016). This allows ecologists to reformulate classic ecological models into stochastic evolutionary birth–death–mutation processes (DeLong & Belmaker, 2019; DeLong & Gibert, 2016; DeLong & Luhning, 2018) to study the feedback between ecological and evolutionary dynamics that emerges out of such a reformulation.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

No data were collected for this study. Code (DeLong, 2022) is available via Zenodo at <https://doi.org/10.5281/zenodo.6974889>.

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## REFERENCES

- Abrams, P. A. 2001. “Modelling the Adaptive Dynamics of Traits Involved in Inter- and Intraspecific Interactions: An Assessment of Three Methods.” *Ecology Letters* 4: 166–75.

- Abrams, P. A., H. Matsuda, and Y. Harada. 1993. "Evolutionarily Unstable Fitness Maxima and Stable Fitness Minima of Continuous Traits." *Evolutionary Ecology* 7: 465–87.
- Champagnat, N. 2006. "A Microscopic Interpretation for Adaptive Dynamics Trait Substitution Sequence Models." *Stochastic Processes and their Applications* 116: 1127–60.
- Champagnat, N., R. Ferriere, and G. B. Arous. 2001. "The Canonical Equation of Adaptive Dynamics: A Mathematical View." *Selection* 2: 73–83.
- Champagnat, N., R. Ferrière, and S. Méléard. 2006. "Unifying Evolutionary Dynamics: From Individual Stochastic Processes to Macroscopic Models." *Theoretical Population Biology* 69: 297–321.
- Champagnat, N., and A. Lambert. 2007. "Evolution of Discrete Populations and the Canonical Diffusion of Adaptive Dynamics." *The Annals of Applied Probability* 17: 102–55.
- Constable, G. W. A., T. Rogers, A. J. McKane, and C. E. Tarnita. 2016. "Demographic Noise Can Reverse the Direction of Deterministic Selection." *Proceedings of the National Academy of Sciences* 113: E4745–54.
- Cortez, M. H., and J. S. Weitz. 2014. "Coevolution Can Reverse Predator–Prey Cycles." *Proceedings of the National Academy of Sciences* 111: 7486–91.
- Costa, M., C. Hauzy, N. Loeuille, and S. Méléard. 2016. "Stochastic Eco-Evolutionary Model of a Prey-Predator Community." *Journal of Mathematical Biology* 72: 573–622.
- Crow, J. F., and M. Kimura. 1965. "Evolution in Sexual and Asexual Populations." *The American Naturalist* 99: 439–50.
- van Daalen, S. F., and H. Caswell. 2017. "Lifetime Reproductive Output: Individual Stochasticity, Variance, and Sensitivity Analysis." *Theoretical Ecology* 10: 355–74.
- Débarre, F., and S. P. Otto. 2016. "Evolutionary Dynamics of a Quantitative Trait in a Finite Asexual Population." *Theoretical Population Biology* 108: 75–88.
- DeLong, J. P. 2022. "jpdelong/GEMs-Gillespie-Eco-Evolutionary-Models-: GEM Code for Matlab." Zenodo. <https://doi.org/10.5281/zenodo.6974889>.
- DeLong, J. P., and J. Belmaker. 2019. "Ecological Pleiotropy and Indirect Effects Alter the Potential for Evolutionary Rescue." *Evolutionary Applications* 12: 636–54.
- DeLong, J. P., and K. E. Coblenz. 2022. "Prey Diversity Constrains the Adaptive Potential of Predator Foraging Traits." *Oikos* 2022: e08800.
- DeLong, J. P., and J. P. Gibert. 2016. "Gillespie Eco-Evolutionary Models (GEMs) Reveal the Role of Heritable Trait Variation in Eco-Evolutionary Dynamics." *Ecology and Evolution* 6: 935–45.
- DeLong, J. P., and T. M. Luhring. 2018. "Size-Dependent Predation and Correlated Life History Traits Alter Eco-Evolutionary Dynamics and Selection for faster Individual Growth." *Population Ecology* 60: 9–20.
- Dieckmann, U., and R. Law. 1996. "The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes." *Journal of Mathematical Biology* 34: 579–612.
- Doebeli, M., Y. Ispolatov, and B. Simon. 2017. "Towards a Mechanistic Foundation of Evolutionary Theory." *eLife* 6: e23804.
- Fussmann, G. F., S. P. Ellner, and N. G. Hairston, Jr. 2003. "Evolution as a Critical Component of Plankton Dynamics." *Proceedings of the Royal Society B* 270: 1015–22.
- Gause, G. F. 1934. *The Struggle for Existence*. Baltimore, MD: Williams and Wilkins (Reprinted 1964 by Hafner).
- Gillespie, D. T. 1977. "Exact Stochastic Simulation of Coupled Chemical Reactions." *The Journal of Physical Chemistry* 81: 2340–61.
- Gillespie, J. H. 1975. "Natural Selection for within-Generation Variance in Offspring Number II. Discrete Haploid Models." *Genetics* 81: 403–13.
- Govaert, L., E. A. Fronhofer, S. Lion, C. Eizaguirre, D. Bonte, M. Egas, A. P. Hendry, et al. 2019. "Eco-Evolutionary Feedbacks—Theoretical Models and Perspectives." *Functional Ecology* 33: 13–30.
- Hastings, A., K. C. Abbott, K. Cuddington, T. Francis, G. Gellner, Y.-C. Lai, A. Morozov, S. Petrovskii, K. Scranton, and M. L. Zeeman. 2018. "Transient Phenomena in Ecology." *Science* 361: eaat6412.
- Hite, J. L., and C. E. Cressler. 2018. "Resource-Driven Changes to Host Population Stability Alter the Evolution of Virulence and Transmission." *Philosophical Transactions of the Royal Society B: Biological Sciences* 373: 20170087.
- Hoyle, A., R. G. Bowers, and A. White. 2011. "Evolutionary Behaviour, Trade-Offs and Cyclic and Chaotic Population Dynamics." *Bulletin of Mathematical Biology* 73: 1154–69.
- Kimura, M. 1965. "A Stochastic Model Concerning the Maintenance of Genetic Variability in Quantitative Characters." *Proceedings of the National Academy of Sciences of the United States of America* 54: 731–6.
- Lande, R. 1976. "Natural Selection and Random Genetic Drift in Phenotypic Evolution." *Evolution* 30: 314–34.
- Lande, R., S. Engen, and B.-E. Saether. 2003. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford: Oxford University Press.
- Lee, D. E., R. W. Berger, J. R. Tietz, P. Warzybok, R. W. Bradley, A. J. Orr, R. G. Towell, and J. Jahncke. 2018. "Initial Growth of Northern Fur Seal (*Callorhinus ursinus*) Colonies at the South Farallon, San Miguel, and Bogoslof Islands." *Journal of Mammalogy* 99: 1529–38.
- Lee, K. P., S. J. Simpson, F. J. Clissold, R. Brooks, J. W. O. Ballard, P. W. Taylor, N. Soran, and D. Raubenheimer. 2008. "Lifespan and Reproduction in *Drosophila*: New Insights from Nutritional Geometry." *Proceedings of the National Academy of Sciences of the United States of America* 105: 2498–503.
- Luhring, T. M., and J. P. DeLong. 2020. "Trophic Cascades Alter Eco-Evolutionary Dynamics and Body Size Evolution." *Proceedings of the Royal Society B: Biological Sciences* 287: 20200526.
- McKane, A. J., and T. J. Newman. 2005. "Predator-Prey Cycles from Resonant Amplification of Demographic Stochasticity." *Physical Review Letters* 94: 218102.
- Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. "How Should we Define 'Fitness' for General Ecological Scenarios?" *Trends in Ecology & Evolution* 7: 198–202.
- Nisbet, R. M., and W. S. C. Gurney. 2004. *Modelling Fluctuating Populations*. Chichester, UK: Wiley.
- Parsons, T. L., A. Lambert, T. Day, and S. Gandon. 2018. "Pathogen Evolution in Finite Populations: Slow and Steady Spreads the Best." *Journal of the Royal Society Interface* 15: 20180135.
- Parsons, T. L., and C. Quince. 2007. "Fixation in Haploid Populations Exhibiting Density Dependence I: The Non-neutral Case." *Theoretical Population Biology* 72: 121–35.

- Parsons, T. L., C. Quince, and J. B. Plotkin. 2010. "Some Consequences of Demographic Stochasticity in Population Genetics." *Genetics* 185: 1345–54.
- Proulx, S. R., and T. Day. 2001. "What Can Invasion Analyses Tell us about Evolution under Stochasticity in Finite Populations?" *Selection* 2: 2–15.
- Reznick, D., L. Nunney, and A. Tessier. 2000. "Big Houses, Big Cars, Superfleas and the Costs of Reproduction." *Trends in Ecology & Evolution* 15: 421–5.
- Shoemaker, L. G., L. L. Sullivan, I. Donohue, J. S. Cabral, R. J. Williams, M. M. Mayfield, J. M. Chase, et al. 2020. "Integrating the Underlying Structure of Stochasticity into Community Ecology." *Ecology* 101: e02922.
- Smith, J. M., and G. R. Price. 1973. "The Logic of Animal Conflict." *Nature* 246: 15–8.
- Stearns, S. C. 1976. "Life-History Tactics: A Review of the Ideas." *The Quarterly Review of Biology* 51: 3–47.
- Taylor, P., and T. Day. 1997. "Evolutionary Stability under the Replicator and the Gradient Dynamics." *Evolutionary Ecology* 11: 579–90.
- Tirok, K., B. Bauer, K. Wirtz, and U. Gaedke. 2011. "Predator-Prey Dynamics Driven by Feedback between Functionally Diverse Trophic Levels." *PLoS One* 6: e27357.
- Vasseur, D. A., P. Amarasekare, V. H. W. Rudolf, and J. M. Levine. 2011. "Eco-Evolutionary Dynamics Enable Coexistence Via Neighbor-Dependent Selection." *The American Naturalist* 178: E96–E109.
- Wilder, S. M., D. G. Le Couteur, and S. J. Simpson. 2013. "Diet Mediates the Relationship between Longevity and Reproduction in Mammals." *Age* 35: 921–7.
- Yoshida, T., N. G. Hairston, Jr., and S. P. Ellner. 2004. "Evolutionary Trade-off between Defence against Grazing and Competitive Ability in a Simple Unicellular Alga, *Chlorella vulgaris*." *Proceedings of the Royal Society B: Biological Sciences* 271: 1947–53.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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