1 **Transient evolutionary attractors alter evolutionary adaptation**

2 *Type of article*: Letter

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Abstract

Stochastic processes such as genetic drift may overwhelm selection and hinder adaptation, but the effect of such stochasticity on evolution via its effect on ecological dynamics is poorly understood. Here we evaluate patterns of adaptation in a population subject to both environmental and demographic stochasticity. We show that stochasticity can alter population dynamics and lead to evolutionary outcomes that are not predicted by traditional eco-evolutionary modeling approaches. 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.

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 (Fisher 1930; Wright 1931) to Nicholson's and Andrewartha and Birch's differing opinions about whether populations were primarily regulated by density-dependent or density-independent (e.g., stochastic) processes (Andrewartha & Birch 1954; Nicholson 1957). Mathematical models have proven to be a valuable tool for studying the various ways that stochasticity can impact ecological (reviewed in (Coulson *et al.* 2004; Black & McKane 2012) and evolutionary (reviewed in (Lenormand *et al.* 2009) dynamics. For example, evolutionary theory has revealed the potential for genetic drift to facilitate adaptation (Wright's "shifting balance" theory; Wright 1931, Coyne et al. 1997) and how stochasticity can shape life history evolution (e.g., "bet hedging" strategies; (Cohen 1966; Childs *et al.* 2010). Ecological theory has shown how stochasticity can excite an underlying deterministic

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50   tendency for a system to oscillate, leading to sustained oscillations (Greenman & Benton 2003; McKane

51   & Newman 2005), and how it can cause systems to shift between different deterministic attractors

52   (Henson *et al.* 1998; Ashwin *et al.* 2012; Abbott & Nolting 2017). However, despite this long-standing

53   interest, there has been is a need for additional work studying how stochasticity affects evolutionary

54   dynamics *through* its effects on ecological dynamics.

55   A number of theoretical approaches for studying the interplay between ecological and

56   evolutionary dynamics have been proposed (reviewed in (Abrams 2001)), including quantitative genetics

57   (QG) and adaptive dynamics (AD) approaches (Abrams *et al.* 1993b; Dieckmann & Law 1996; Geritz *et al.*

58   1998; Abrams 2001). While there are important differences between the two methods, for example in

59   their assumptions about reproduction and the relative timescales of ecological and evolutionary

60   processes, their predictions for eco-evolutionary dynamics are often identical. This is because, in both

61   approaches, the direction of selection is determined by the fitness gradient: the derivative of individual

62   fitness (W) with respect to the evolving trait (x). The dynamics of the mean trait (x) are given by

63   (Abrams *et al.* 1993b; Abrams 2001; Doebeli *et al.* 2017):

64
$$\frac{dx}{dt} \propto \left(\frac{\partial W}{\partial x} \right)_{x=x}.$$

65   An equation of this form can be arrived at either through the equations for trait change in quantitative

66   genetics (Lande 1976; Abrams *et al.* 1993b), or through a consideration of stochastic birth-death

67   processes (Dieckmann & Law 1996). Given that individual fitness will be affected by ecological

68   interactions, there is broad scope for eco-evolutionary feedbacks to affect the dynamics of both the

69   ecological and evolutionary system in non-intuitive ways (Fussmann *et al.* 2003; Cortez & Ellner 2010;

70   Vasseur *et al.* 2011; Cortez 2016).

71   Given the key role of ecological dynamics in shaping the fitness gradient, stochasticity that alters

72   ecological dynamics may also influence adaptation. However, both the QG and AD approaches typically

73   assume that populations are large so that demographic stochasticity can safely be ignored. Studies that

109 have included demographic stochasticity have shown that it can alter the eco-evolutionary dynamics

110 predicted by QG and AD approaches (Proulx & Day 2002); for examples, demographic stochasticity can

111 delay or prevent evolutionary branching due to disruptive selection (Claessen *et al.* 2007; Wakano &

112 Iwasa 2013) and it can lead to the evolution of pathogens with lower transmission and virulence

113 (Humplik *et al.* 2014; Parsons *et al.* 2018).

114 To study how stochasticity can influence the path and pace of adaptation by altering ecological

115 dynamics, we use Gillespie eco-evolutionary models [GEMs] (DeLong & Gibert 2016; DeLong & Luhring

116 2018; DeLong & Belmaker 2019), to generate the ecological and evolutionary dynamics through the

117 simulation of stochastic birth-death processes (Dieckmann & Law 1996; Champagnat *et al.* 2006; Doebeli

118 *et al.* 2017). Specifically, we compare the ecological and evolutionary dynamics produced by GEMs to

119 deterministic expectations based on the quantitative genetics (QG) approach (Abrams *et al.* 1993b, a).

120 Demographic stochasticity is built into the structure of the GEMs through stochasticity in the birth and

121 death process. We study the eco-evolutionary dynamics of a simple ecological model of logistic growth

122 in two scenarios: 1) varying the location of the ecological equilibrium (i.e., carrying capacity) and 2)

123 introducing culling that is unrelated to an individual's traits. We show that demographic stochasticity

124 often prevents populations from reaching the expected evolutionary equilibrium, but we find that, just

125 as often, the realized evolutionary outcome can still be understood using the deterministic equations. In

126 particular, we show that stochasticity can trap populations at "transient evolutionary attractors" (TEAs),

127 which we define as density-dependent fitness optima that are temporary because they change location

128 as the population grows or declines. These TEAs represent peaks on an adaptive landscape that are not

129 identical to the deterministic expectation generated for equilibrium conditions. We suggest that these

130 TEAs may play an important role driving evolutionary dynamics in many natural systems, and more

131 generally, that understanding transient evolutionary phenomenon may provide new insights into how

132 populations evolve.

212 **Material and methods**

213 *Deterministic eco-evolutionary dynamics:* The quantitative genetics approach to modeling eco-

214 evolutionary dynamics allows for ecological and evolutionary dynamics to occur on similar timescales

215 (Abrams 2001); this approach derives the fitness gradient equation as an approximation of the

216 quantitative genetics equations of Lande (1976) that holds assuming that the trait distribution is

217 unimodal and that the variance in fitness is greater than the variance in the trait (Taper & Case 1992;

218 Abrams *et al.* 1993a, b; Abrams 2001). An identical expressions can also be derived from the dynamics of

219 genotypes via the Price equation (Taylor & Day 1997; Day & Gandon 2006). The rate of evolutionary

220 change is determined by the additive genetic variance; this value is often held constant but can be

221 allowed to change dynamically (Abrams et al. 1993b, Taylor & Day 1997).

222 To investigate how stochasticity influences evolutionary dynamics, we consider a simple model

223 for density-dependent population growth that can provide deterministic baseline expectations:

224 $$\frac{dR}{dt} = (b_{max} - b_s R)R - (d_{min} + d_s R)R, \qquad \text{(Equation 1)}$$

225 where R is population abundance, b_{max} is the maximum birth rate, d_{min} is the minimum death rate, and b_s

226 and d_s characterize the effects of population abundance on the realized birth and death rates,

227 respectively. This model is a simple expansion of the logistic model, with maximum rate of population

228 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

229 logistic model this way to allow us to simulate the ecological dynamics as a stochastic birth-death

230 process. We consider the case where b_{max} is evolving and is connected to mortality through a classic life

231 history trade-off between reproduction and mortality (Stearns 1976). This trade-off has been widely

232 demonstrated across plants, invertebrates, and vertebrates (REFS); more practically, positing such a

233 trade-off facilitates our analysis because it leads to an evolutionary equilibrium where fitness is

234 maximized.

235 Using the QG approach, the dynamics of the population mean trait, $\overline{b_{max}}$, are given by

270 $$\frac{d\overline{b_{max}}}{dt} = V\left(\frac{\partial W}{\partial b_{max}}\right)_{b_{max}=\overline{b_{max}}},$$

271 where V is the product of narrow-sense heritability and additive genetic variance in b_{max}, $W = R/R$ is

272 the per-capita growth rate (i.e., individual fitness), and $\left(\frac{\partial W}{\partial b_{max}}\right)_{b_{max}=\overline{b_{max}}}$ is the fitness gradient

273 evaluated at the mean trait. The fitness gradient will equal zero at the evolutionary equilibrium. Given

274 equation (1) above, the fitness gradient is equal to $1 - d'_{min}\left(\overline{b_{max}}\right)$, which implies that the minimum

275 death rate must be an increasing function of the maximum birth rate for an evolutionary equilibrium to

276 exist. For any equilibrium to represent a fitness maximum requires $\frac{\partial^2 W}{\partial b_{max}^2} = -d''_{min}(b_{max}) < 0$, which

277 implies that the minimum death rate must be an accelerating function of maximum birth rate. As such,

278 we assume that $d_{min} = cb_{max}^2$, making the equation for the evolutionary dynamics

279 $$\frac{d\overline{b_{max}}}{dt} = V\left(1 - 2c\overline{b_{max}}\right)$$ (Equation 2)

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

281 evolutionary equilibrium:

282 $$\left(R = \frac{\overline{b_{max}} - \overline{d_{min}}}{b_s + d_s}, \overline{b_{max}} = \frac{1}{2c}\right).$$ (Equation 3)

283 We borrow the terminology of the adaptive dynamics literature and call this value of $\overline{b_{max}}$ an

284 evolutionarily stable strategy (ESS), since it is an evolutionary equilibrium where fitness is maximized.

285 *Stochastic eco-evolutionary dynamics:* GEMs simulate ecological dynamics through a stochastic birth-

286 death process (DeLong & Gibert 2016; DeLong & Luhring 2018; DeLong & Belmaker 2019). GEMs build

287 on the standard Gillespie algorithm for simulating ODE models where demographic stochasticity

288 (random variation in the sequence and number of demographic events) influences the outcomes

289 (Gillespie 1977; Yaari *et al.* 2012) by incorporating demographic heterogeneity (variation among

290 individuals in demographic traits. Every individual in the simulation has a trait value drawn from a

291 distribution with known mean and variance, with the type of distribution depending on nature of the

314 trait. In a GEM, an individual's trait value determines its probability of giving birth or dying; evolutionary

315 dynamics thus emerge out of the stochastic births and deaths of individuals within the population

316 (Dieckmann & Law 1996; Champagnat *et al.* 2006; Doebeli *et al.* 2017).

317   GEMs function in an iterative cycle of birth and death events. Rather than taking a constant

318 parameter value, as in a standard Gillespie simulation, the random draw of a trait from the trait vector is

319 used either as a parameter or as a trait that influences a parameter. Thus, each individual experiences a

320 particular probability of birth or death depending on their traits. Once the individual is chosen and the

321 rate terms are calculated, an event is randomly chosen 'wheel-of-fortune' style. If the event is a death,

322 that individual (and its trait) are removed from the population. If the event is a birth, a new individual is

323 added to the population given some rule for heritability of that trait (Appendix S1). As a GEM is running,

324 the loss and addition of individuals in the population affects both population dynamics and the dynamics

325 of both the mean and variance of the trait distribution. Populations gradually lose individuals with high

326 likely of mortality and gradually add individuals with higher likelihood of births, generating natural

327 selection without needing to specify explicit equations for the trait dynamics or without needing to

328 identify explicitly the expected trait equilibria such as an ESS.

329   The inclusion of both demographic heterogeneity and demographic stochasticity in GEMs has

330 two potentially important effects on the predictions these models make. First, it is increasingly

331 recognized that variation in traits among individuals can have important effects on ecological and

332 evolutionary dynamics, even if those differences are not heritable ((Kendall *et al.* 2011; Stover *et al.*

333 2012; Cressler *et al.* 2017). Second, when trait differences do lead to differences in the expected fitness

334 of those individuals (Figure 1A), demographic stochasticity causes individuals to randomly deviate from

335 their expected fitness (van Daalen & Caswell 2017). For example, Banks and Thompson (Banks &

336 Thompson 1987) assessed lifetime reproductive success of the damselfly *Coenagrion puella* with respect

337 to individual head width (Figure 1B). Although there was a clear fitness-maximizing value of head width

359   in the damselfly population, the realized lifetime reproductive success of individuals was quite variable,

360   and many individuals with the optimal head width realized relatively low fitness (Figure 1B). On top of

361   individual variation in realized fitness, demographic stochasticity has long been recognized to have

362   important effects on the dynamics of adaptation, for example through genetic drift (Lenormand *et al.*

363   2009) or the loss of high-fitness genotypes (Crespi 2000).

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

365   Comparison 1: We first examined the role of individual variation in b_{max} on the ecological

366   dynamics of this model when no evolution was possible. To do this, we set heritability $h^2 = 0$ and

367   introduced variation in traits in the population with CV = 0.3. Because in our model, the d_{min} is locked to

368   b_{max}, variance in b_{max} will drive variance in d_{min}. We therefore broke this apart to evaluate the effect of

369   variance in each parameter on ecological dynamics separately. We examined whether variation in

370   neither trait, b_{max} alone, d_{min} alone, or both traits combined, influenced the dynamics, respectively, by

371   eliminating variance altogether; by allowing variance in b_{max} but holding d_{min} constant; by allowing

372   variance in d_{min} but holding b_{max} constant (achieved by first allowing variation in b_{max} to drive variation in

373   d_{min} but then re-setting b_{max} to the mean); and by allowing both to vary together as normal. This

374   examination also confirmed whether in the absence of trait variance that the GEM dynamics reduced to

375   a standard Gillespie simulation of the ecological model (Equation 1). We used $b_s = d_s = 0.04$ for this

376   simulation.

377   Comparison 2: We next evaluated differences between the GEM and QG approaches by

378   comparing outcomes across different values of b_s and d_s, which set the strength of density dependence

379   on birth rates and death rates, respectively (Equation 1). Varying these two parameters effectively

380   changes the carrying capacity of the system such that starting at any given population size means

381   starting at a different distance from equilibrium. We expected that these simulations would vary in the

382   amount of stochastic loss of trait variation because of the different rates populations would grow at the

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388 start of the simulation. We initiated these populations at a population abundance of five and allowed

389 them to grow.

390   Comparison 3: Finally, we asked how harvesting a population that has already achieved an eco-

391 evolutionary equilibrium would cause it to evolve. The deterministic model for the population dynamics

392 is the following:

393
$$\frac{dR}{dt} = (b_{max} - b_s R)R - (d_{min} + d_s R)R - x \max(0, R - R_{cull}).$$

394 Under this model, we cull the population at the rate x whenever $R > R_{cull}$. As $x \to \infty$, the equilibrium

395 $R \to R_{cull}$. As we show in the Appendix, because this culling is trait-independent, the evolutionary

396 dynamics for the mean trait $(d\overline{b_{max}}/dt)$ are still given by equation (2) above. Thus, harvesting here is

397 functioning as a form of environmental stochasticity. We do this with an intermediate level of density

398 dependence with three levels of culling.

399 *Modeling details:* For Comparisons 1 and 2, populations were initialized with five individuals with mean

400 traits $\overline{b_{max}} = 1.8, \overline{d_{min}} = 0.3$ and $c = 0.0926$ (since $d_{min} = cb_{max}^2, c = \frac{d_{min}}{b_{max}^2} = \frac{0.3}{1.8^2} = 0.0926$). The ESS

401 $\overline{b_{max}}$ for this system is 5.4, which means the ESS $\overline{d_{min}}$ is 2.7. The CV of the evolving trait in the initial

402 population was set at 0.3, such that the initial variance in b_{max} was 0.29. Heritability was fixed at 0.75.

403 We make density dependence in births and deaths symmetrical, so $b_s = d_s$, and set these equal to 0.075,

404 0.0375, and 0.01875 to generate a gradient in density dependence. Since the equilibrium abundance

405 depends on the value of b_{max} (Equation 3), the initial equilibrium abundances (K_{init}) at $b_{max}=1.8$ were

406 10, 20, and 40 across the three scenarios; at the ESS value of $\overline{b_{max}}=5.4$, the expected equilibrium

407 abundances (K_{ESS}) were 18, 36, and 72. In the Appendix, we show the results of simulations that held

408 density-dependence fixed at $b_s = d_s = 0.375$ and varied the trade-off parameter c between 0.06 and

409 0.12. For Comparison 3, populations were initialized with 72 individuals with $\overline{b_{max}} = 5.4$ (thus at the

410 eco-evolutionary equilibrium for $b_s = d_s = 0.01875$). Individuals were culled at random with respect to

440 their traits with a culling rate of $x = 1000$ (which ensures that the population size rapidly approaches

441 N_{cull}) and N_{cull} values of 50, 30, or 10. We ran each simulation for 400 time steps, long enough to

442 clearly identify its attractor, and we simulated 50 stochastic replicates for each parameter set.

443   To evaluate patterns in individual fitness across GEM simulations, we tracked the number of

444 reproductive events and the lifespan for each individual. This allowed us to visualize the realized

445 relationship between each individual's b_{max} and lifetime reproductive success, akin to Figure 1B. We do

446 this for the initial population (born before time step 1) and the population toward the end of the

447 simulation (born after time step 350). For the latter, we only included individuals that died before the

448 end of the simulation.

449 **Results**

450 *Comparison 1:* Reducing heritability to zero effectively eliminates evolution by natural selection,

451 revealing how trait variation *per se* alters the dynamics of the system (Figure 2). Variation in b_{max} alone

452 reduced the equilibrium abundance of the population. Variation in d_{min} alone had little effect on the

453 population, but combined with b_{max}, d_{min} reduced the equilibrium abundance of the population even

454 more (by about 7% below the expected equilibrium). This result indicates that trait variation *per se* is

455 one factor that may limit the populations in our simulations from achieving the expected ecological

456 equilibria.

457 *Comparison 2:* In our second set of simulations, in which we varied only the strength of density

458 dependence, we found that all populations grew and evolved b_{max} in the direction of the ESS (Figure 3,

459 2nd and 4th rows). Although no population was able to grow or evolve as fast as expected from QG

460 (Figure 3, 1st and 2nd rows), the population experiencing the least density dependence converged to the

461 expected eco-evolutionary equilibrium.

462   We also found that populations with stronger density dependence (i.e., higher values of b_s and

463 d_s and lower K_{init} values) experienced greater initial loss of trait variation (Figure 3, third row). This loss

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478   of variation slows the pace of evolution relative to the QG expectation. At intermediate and low density

479   dependence, the initial loss of trait variation was more temporary, allowing populations to recover from

480   the effects of low-density stochasticity and continue moving in the direction of the ESS. As expected, the

481   effects of stochasticity were noticeably higher for small populations, with considerably more variation in

482   abundances through time for populations with the highest density dependence (Figure 3, left column).

483   However, all populations displayed considerable individual demographic stochasticity (Figure 3, bottom

484   row), manifested as large differences in lifetime reproductive success among individuals with the same

485   trait values. In addition, the peak in the observed lifetime reproductive success distribution for the

486   population with the most severe density dependence (bottom left panel) occurred to the left of the ESS,

487   while the population with mildest density dependence showed a peak that aligned with the ESS.

488   To help understand this result, we calculated the expected lifetime reproductive success of an

489   individual from the model:

490   $R_0 = \frac{(b_{max} - b_s R)}{(d_{min} + d_s R)}.$ (Equation 4)

491   The value of b_{max} that maximizes R_0 is given by the solution of the equation $\frac{\partial R_0}{\partial b_{max}} = 0$:

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

493   Note that the value of b_{max} that maximizes expected lifetime reproductive success is not necessarily the

494   same as the ESS value (although when R is at an equilibrium, the values are the same). In particular, this

495   value depends on the current population size. We term this transient peak on the fitness landscape a

496   "transient evolutionary attractor" (TEA), because it changes as the population moves through its

497   transient dynamics. Re-examining the observed lifetime reproductive success values, it is clear that the

498   peak of the observed distribution is often centered on these TEAs (Fig. 3, bottom row), and that the

499   observed evolutionary trajectory for b_{max} often appears to be approaching this TEA, rather than the ESS

500   (Fig. 3, second row).

506   If we visualize the fitness landscape using lifetime reproductive success, we can see how this

507 landscape changes as the populations grew, generating TEAs that shifted along with the population

508 (Figure 4). Populations moved along these fitness contours as the population grew toward its ecological

509 equilibrium. Population trajectories, however, showed considerable stochastic variation in abundance

510 when density dependence was strong, preventing approach to either the local TEA or the ESS, while

511 populations with low density dependence displayed a smooth, direct approach toward the ESS.

512 *Comparison 3:* In our third set of simulations, we applied a persistent cull to populations that had

513 already achieved their ESS trait and abundance values. The population size changed almost immediately

514 so that $R \approx R_{cull}$, whereas the evolutionary trajectory showed a clear movement of the mean b_{max}

515 away from the ESS. Again, we can ask what value of b_{max} maximizes expected reproductive success. The

516 expected lifetime reproductive success under culling is

517 $$R_0 = \frac{b_{max}-b_s R}{d_{min}+d_s R+x \max\left(0,1-\frac{R_{cull}}{R}\right)}. \hspace{3cm} \text{(Equation 6)}$$

518 Assuming that $R \approx R_{cull}$, the value of b_{max} that maximizes R_0 is given by Eq. (5) above. Fig. 5 shows

519 clearly that the population mean b_{max} evolved to the population-specific TEAs that depended on the

520 population size the cull produced (Figures 5,6). Rather than returning to the ESS, populations that were

521 reduced to a lower abundance shifted their path immediately to head upslope toward the abundance-

522 determined TEA and away from the ESS (Figure 6). The populations followed a path of adaptation

523 specific to the current transient state, as generated by Equation 5, not the path generated by

524 equilibrium conditions.

525 **Discussion**

526 Evolutionary theory today encompasses a wide range of modeling techniques and frameworks that

527 facilitate an understanding of how populations evolve and adapt to their environments (Lande 1982;

528 Abrams *et al.* 1993a; DeAngelis & Mooij 2005; Coulson *et al.* 2006; Ellner & Rees 2006; Lion 2017; de

529 Vries & Caswell 2019; Govaert *et al.* 2019). (Doebeli *et al.* 2017) has argued that a proper mechanistic

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534 foundation for evolutionary theory should be stochastic birth-death processes, rather than fitness.

535 However, while such models can readily be simulated, as we do here, deterministic approximations of

536 such processes are required to make limiting assumptions, such as a separation of ecological and

537 evolutionary timescales, weak selection, small mutation, or large population size (Dieckmann & Law

538 1996; Champagnat *et al.* 2006; Doebeli *et al.* 2017; Parsons *et al.* 2018). Here we show that, even when

539 these assumptions are not met, the resulting stochastic eco-evolutionary dynamics can still be

540 understood from a consideration of the deterministic approximation. In particular, we show that

541 demographic heterogeneity and demographic stochasticity can keep populations away from an

542 expected ecological equilibrium, and that under such conditions the population mean traits can evolve

543 towards transient evolutionary attractors. The eco-evolutionary dynamics and the pace and path of

544 evolution, then, are qualitatively and quantitatively different from predictions that overlook transient

545 periods of evolution, such as classic adaptive dynamics approaches that assume a separation of

546 ecological and evolutionary timescales (Geritz *et al.* 1998; Abrams 2001). The transient evolutionary

547 dynamics that unfolded during our GEM simulations here responded to underlying fitness contours that

548 are invisible with an equilibrium lens but that lay out a straightforward evolutionary path that transient

549 populations can follow. With the rapid environmental change and direct human impact that disrupts

550 populations throughout the world today, we agree that theories of evolution that focus on stochastic

551 birth-death processes, and the transient, non-equilibrium dynamics of such processes, will provide

552 crucial new insights into the adaptation of wild populations.

553 In addition to the effects caused by the transient fitness landscapes, our results indicate that the

554 presence of individual trait variation (and the resulting demographic heterogeneity (Kendall *et al.* 2011;

555 Stover *et al.* 2012)), although required for evolution to proceed, can itself change the ecological

556 dynamics. In our case, this variation simultaneously facilitated evolution by providing raw material upon

557 which selection could act and maintained the system in a transient state (i.e., a state in which

577 equilibrium has not been attained) such that the expected evolutionary equilibrium could not be

578 attained. Individual demographic stochasticity, abundantly displayed in our results, clearly influenced

579 the relationship between fitness and traits, causing some individuals with low fitness traits realized high

580 fitness, while some individuals with high fitness traits realized low fitness (Figures 3 and 5, bottom row).

581 This effect should result in a flattened fitness gradient relative to the expectations from quantitative

582 genetics, greatly reducing the rate of evolution (Cressler et al. 2017). Finally, demographic stochasticity

583 generated heightened variation in population size for small populations, both keeping populations in

584 transient states and leading to substantial initial loss of genetic variation. Examination of the population

585 dynamics in the systems with lower carrying capacities (Figure 3) indicate substantially more variation in

586 population sizes, reflecting high stochasticity. All together, these forces substantially slowed evolution

587 relative to expectations generated from classic assumptions of deterministic evolutionary theory.

588   Increasing evidence indicates that ecological dynamics can play a crucial role in shaping

589 evolution (Pimentel 1961; Grant & Grant 2002; Yoshida et al. 2004; Hairston, Jr. et al. 2005; Schoener

590 2011). Furthermore, evolution within systems not at equilibrium, and rather displaying transient

591 dynamics (Hastings et al. 2018), can alter the ecological dynamics and therefore the selective forces

592 acting on the population (Fussmann et al. 2003; Yoshida et al. 2003; Cortez & Weitz 2014). Our results

593 further this finding, demonstrating that even simple, single-species models can facilitate not just eco-

594 evolutionary dynamics but generate transient attractors that may compete with the overall evolutionary

595 attractor in the system (i.e., the ESS). By taking into account the full consequences of individual variation

596 and stochasticity, we may generate more realistic predictions for evolution. We do not, however,

597 suggest that TEAs will be present in all systems. The minimum requirement for a TEA is that the

598 expression $\frac{\partial\text{fitness}}{\partial\text{trait}} = 0$ must actually have a solution, otherwise there is neither an ESS nor a TEA.

599 Furthermore, if an expression for a trait optimum includes population size, then the optimum is not the

600 same at equilibrium as it is away from equilibrium. The non-equilibrium peak is the TEA, and the

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613 equilibrium peak is the ESS. In our Equation 5, a fitness maximum exists and population abundance R is

614 present in the expression, generating a TEA. Thus, to the extent that these conditions are met, likely in

615 most cases of density-dependent demographics with some sort of trade-off among fitness related traits,

616 TEAs may be a common feature of evolutionary pathways.

617   One of the most non-intuitive results here is that culling can dramatically alter the evolutionary

618 dynamics from the expectation. As we show in the Appendix, trait-independent culling does not alter

619 the expected evolutionary dynamics, and thus we would expect that a population whose trait was

620 already at the ESS would not evolve away from it. And yet, we see that trait evolution moves away from

621 the ESS and towards the TEA (Fig. 5) as the population abundance decreases. Our results may have

622 important implications for managed populations. Economically important populations, from fisheries to

623 ungulates and invasive species, may show substantial changes in traits in response to random or trait-

624 biased harvesting (Darimont *et al.* 2009). In Windermere pike (*Esox lucius*), for example, harvesting is

625 thought to have altered the fitness landscape and generated selection away from the direction driven by

626 the natural setting (Edeline *et al.* 2007). This evolutionary outcome could represent both the direct

627 selective effects of harvesting itself but also the presence of a transient attractor that competed with an

628 ESS attractor, since harvesting maintained populations in a transient state. Understanding evolution in

629 such populations may require a disequilibrium (transient) approach, because harvested populations are

630 by definition being held below their potential equilibrium. To the degree that these populations show

631 density dependence in their birth or death rates, similar to but not necessarily following the birth-death

632 logistic model, they are likely to also display TEAs that could draw their traits away from the starting

633 values, whether the initial trait distributions are at the ESS value or not. Harvesting our simulated

634 population at something near the maximum sustainable yield, for example, could nearly halve the

635 fecundity of the population, even without harvesting having a direct selective effect. In the birth-death

636 logistic model (Equation 1), the ecological equilibrium depends on these traits, and so evolution toward

Deleted: once the expression is found for an ESS trait, the abundance of the population must not cancel out.

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Commented [CC9]: Is it worth discussing the fact that our results are a bit counter to most evolutionary theory on the effect of harvesting?. That is, harvesting is typically predicted to favor the evolution of faster life histories (higher birth and death rates). We don't see that here because the cull mortality is dependent on the population being larger than the R_cull. That is, in most models of harvesting, it is assumed that harvesting happens regardless of the population size, rather than assuming that harvesting only happens when the population size is > R_cull. Mathematically, it is the difference between the R0 being $\frac{bmax - bs\,R}{dmin + ds\,R + x}$
In a classic harvesting model and
$\frac{bmax - bs\,R}{dmin + ds\,R + x \max\left(0, 1 - \frac{Rcull}{R}\right)}$
In our model. Note that the term involving the x is always present in the former, but disappears when R <= Rcull in the later. Thus, the primary effect of culling in our model is to reduce the strength of density-dependence, whereas culling functions as an extra source of mortality in general.

To really talk about this, we will likely need to address the difference between *culling* and *harvesting*.

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640   the TEA would further alter the system and potentially lead to unexpected shifts in both traits and

641   abundance.

642   Studying the evolutionary process from the perspective of stochastic birth-death processes

643   increases the opportunity for profitable cross-pollination between ecological and evolutionary theory

644   (Doebeli *et al.* 2017). In particular, while other authors have used approaches very similar to GEMs to

645   test the predictions of classic evolutionary theory (e.g., (Claessen *et al.* 2007), GEMs provide a natural

646   and straightforward way to reformulate classic ecological models into stochastic evolutionary birth-

647   death processes (DeLong & Gibert 2016; DeLong & Luhring 2018; DeLong & Belmaker 2019), allowing

648   ecologists and evolutionary biologists to study the feedback between ecological and evolutionary

649   dynamics that emerges out of such a reformulation.

650   In conclusion, our results indicate that stochastic birth-death processes, by introducing

651   individual variation and demographic stochasticity, can produce evolutionary trajectories that differ

652   significantly from expectations based on deterministic approaches, revealing powerful competing

653   evolutionary attractors (TEAs) that have not factored into much (if any) current thinking on the pace and

654   path of adaptation. However, we also find that these TEAs can still be understood on via the

655   deterministic approximations, helping to reveal both the utility and the limitations of such

656   approximations. Becoming aware that evolution is relatively fast, and that many populations are in

657   transient states rather than equilibrium states, may be essential for a fuller understanding of

658   adaptation.

659   **Acknowledgements**

660

662   **References**

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946 Figure 1. Variation in the relationship between traits and fitness. A. A depiction of how stochasticity and

947 heterogeneity map on to the relationship between traits and fitness. B. An example of this relationship

948 with the damselfly *Coenagrion puella* (Banks & Thompson 1987). These data show that lifetime

949 reproductive success (here lifetime clutches) may reach a peak at some intermediate trait value.

950 Simultaneously, individuals may vary dramatically in their realized fitness despite an expected fitness

951 outcome.

952

953 Figure 2. Results of a GEM simulation of the birth-death logistic model evaluating the isolated effects of

954 trait variance on the dynamics. In these simulations, variance in the linked birth and death rates were

955 isolated, and heritability was set to zero. In the leftmost panel, all trait variance was removed, causing

956 the simulations to collapse on the non-evolutionary ordinary differential equation solution. This

957 indicates that the GEM effectively collapses to a standard Gillespie simulation. In the second panel from

958 the left, variance in mortality was removed by setting it equal to the mean value given its link to births

959 (see main text). In the third panel, we removed variance in births while retaining it in deaths. In the

960 fourth panel, variance in both traits was retained. This final panel indicates that trait variance

961 (demographic heterogeneity) alters the ecology of the system, lowering the abundance at equilibrium

962 relative to that expected from the mean traits themselves. The median (dark solid line) and middle 50%

963 (shaded area) of simulations are shown.

964

965 Figure 3. Gillespie eco-evolutionary model (GEM) simulations of the birth-death logistic model. The rows

966 show from top to bottom population abundance (y axis limits vary), mean b_{max}, variance in b_{max}, and

967 lifetime reproductive success (product of expected births and expected survival). The columns show

968 three levels of density dependence in birth and death rates (values of b_s and d_s), decreasing in strength

969 from left to right (0.1, 0.04, 0.005). The median and middle 50% of GEM trajectories are in purple and

973 light purple, respectively. The quantitative genetics (QG) solution is in bold orange and the evolutionary

974 stable strategy (ESS) is shown as a dashed orange line in the top two rows and a solid vertical line in the

975 bottom row. The initial trait and equilibrium abundance are shown with dashed black lines, and the

976 transient evolutionary attractors (TEAs) are in pink (dashed in row two and solid vertical in row four).

977 Lifetime reproductive success at the beginning (gray dots) and at the end of the simulation (black dots)

978 as a function of b_{max} include only individuals that completed their lives.

979

980 Figure 4. Fitness landscapes of the systems represented in Figure 3. Variation in the fitness landscape

981 caused by changes in abundance are shown with the sequences of black dots, such tha the landscapes

982 tend to get flatter toward the ESS and the ecological equilibrium. The gray line connects the transient

983 evolutionary attractors (TEAs) across density levels. The simulations were initiated at the abundance and

984 trait values indicated by the red dot, with the populations proceeding along the orange line. The

985 evolutionary stable strategy (ESS) of the system is shown by the blue dot, and the competing TEA at the

986 population size occurring by the end of the simulation is shown in teal. From left to right, the panels

987 show the trajectories from Figure 3, with decreasing density dependence and thus a higher carrying

988 capacity toward the right. When density dependence is high, and populations remain relatively small,

989 substantial stochasticity limits evolution and generates erratic population abundances that never can

990 fully reach either the ESS or the TEA. At lower density dependence and higher population sizes,

991 however, the populations can more smoothly find their way toward the ESS.

992

993 Figure 5. Results of Gillespie eco-evolutionary model (GEM) simulations of the birth-death logistic model

994 for populations culled to five individuals from the starting point at the ESS trait and the equilibrium

995 abundance. From left to right, the population is culled more severely (to 100, 50, and 5 from left to

996 right). Layout the same as in Figure 3.
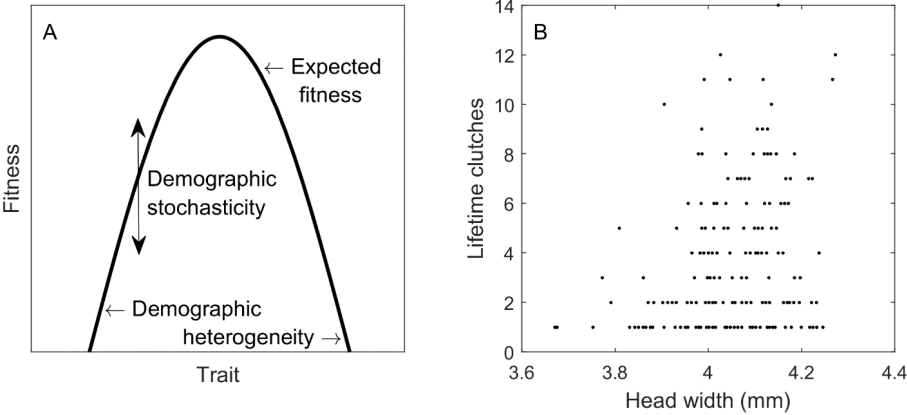
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1001   Figure 6. Transient fitness landscapes for the birth-death logistic model with three levels of culling and

1002   the weakest density dependence ($b_s = d_s = 0.01$). The overall layout is the same as in Figure 3. The

1003   colored lines represent the trajectories from Figure 5, with orange being a cull to 100, purple being a cull

1004   to 50, and green being a cull to 5 individuals. Each population is evolving toward their local TEA (color

1005   coded to match trajectories). The populations started at the ESS trait and equilibrium abundance (blue

1006   dot).

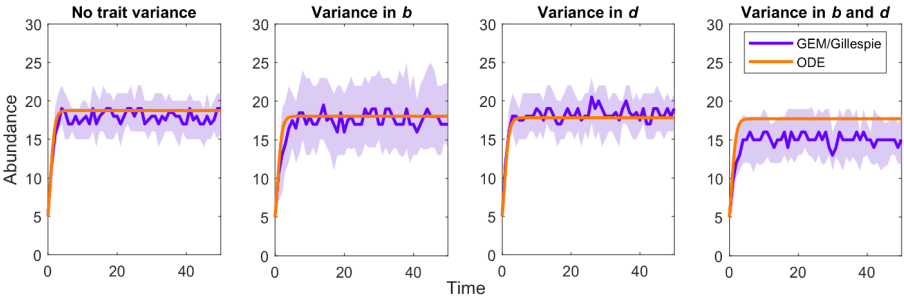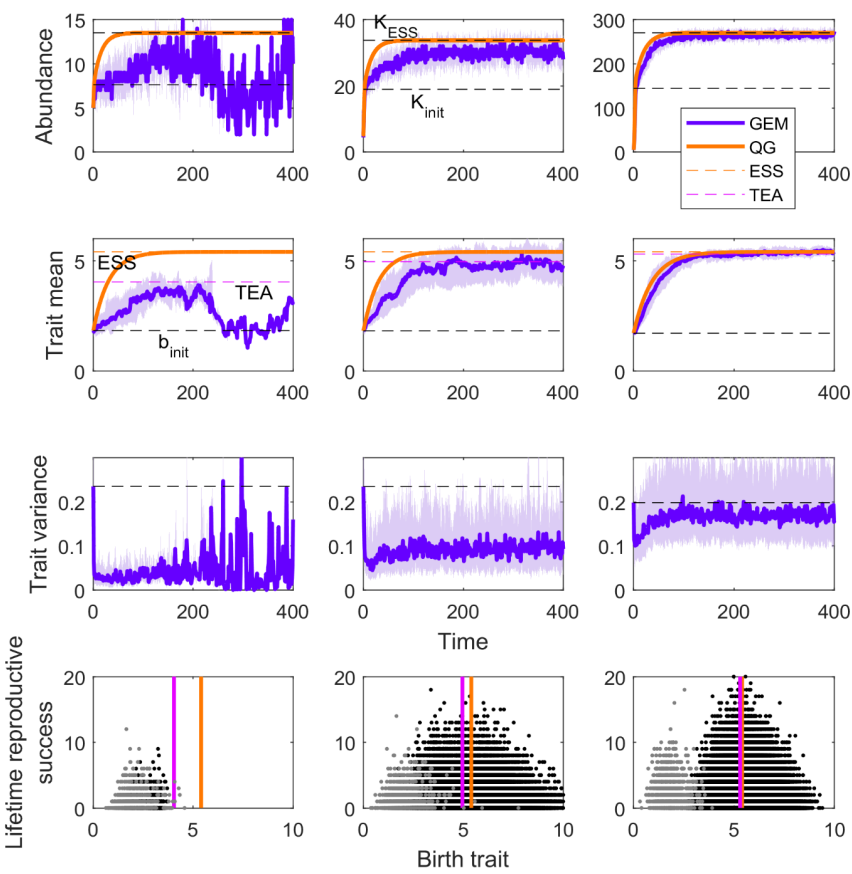1007

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1010   Figure 1.

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1014   Figure 2.

No trait variance   **Variance in *b***   **Variance in *d***   **Variance in *b* and *d***

Legend: GEM/Gillespie, ODE

Y-axis: Abundance
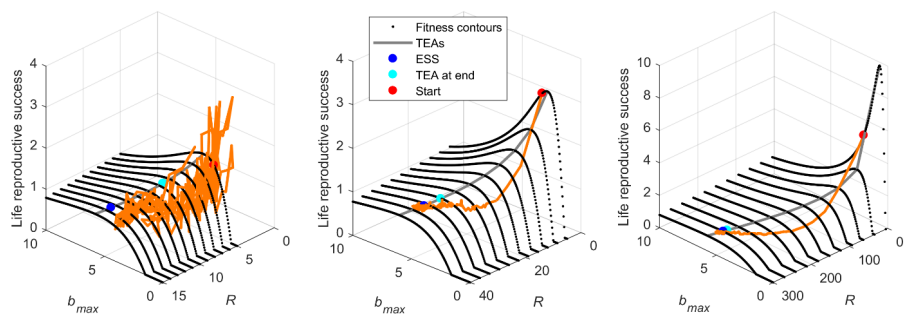X-axis: Time

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1017   Figure 3.

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Figure 4.
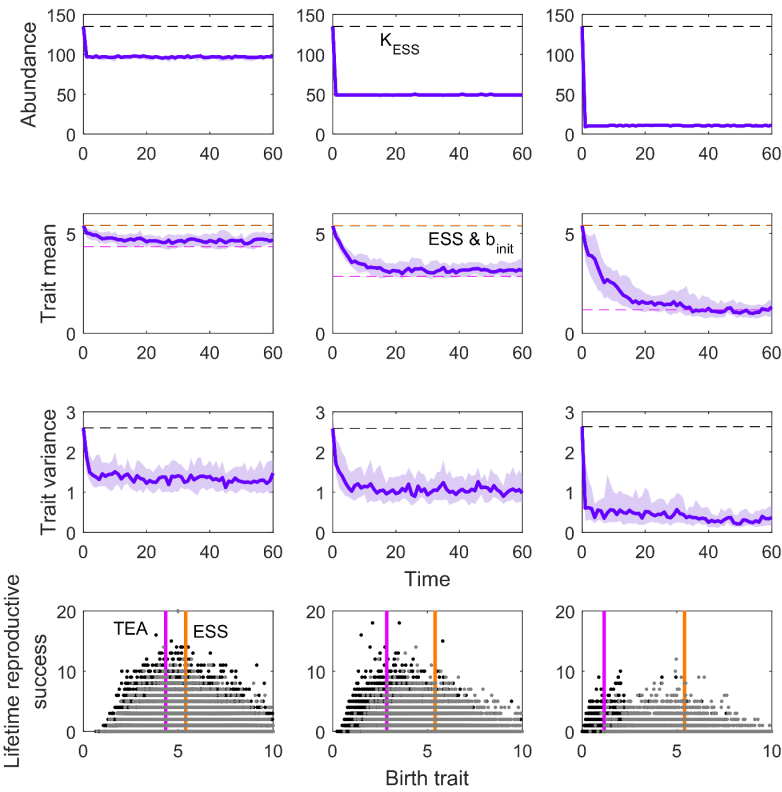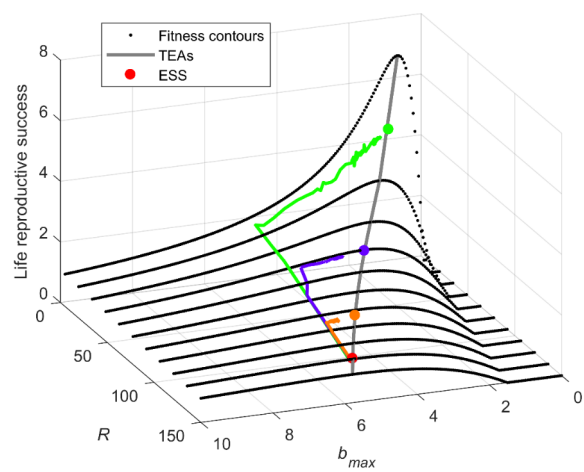
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1025   Figure 5.

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1029   Figure 6.

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1034 **DeLong and Cressler, "Transient evolutionary attractors alter evolutionary adaptation"**

1035 **Appendix S1. Heritability rules.**

1036 In a GEM, births and deaths occur through an iterative, stochastic process given an underlying

1037 model. In the event of a birth, a new individual is added to the population given some rule for

1038 heritability of that trait. In these simulations, we follow the heritability rules derived and

1039 presented in (DeLong & Luhring 2018; DeLong & Belmaker 2019) with the change that we are

1040 not using here the weighted mean for the parental trait.

1041 If a birth event occurs in a GEM, an offspring trait is randomly drawn from a lognormal

1042 distribution with a mean of $\mu_{offspring} = (1 - h^2)\overline{b_{max}} + h^2 b_{max}$, where b_{max} is the actual

1043 trait of the current parent, $\overline{b_{max}}$ is the current population mean, and h^2 is narrow-sense

1044 heritability. The standard deviation of this distribution is given as $\sigma_{offspring} =$

1045 $\sqrt{(1 - h^{2^2})[(1 - h^2)\sigma_0 + h^2\sigma_t]}$, where σ_0 is the standard deviation in b_{max} in the initial

1046 population and σ_t is the standard deviation in b_{max} currently. This trait is then added as a new

1047 element of the trait distribution, increasing the size of the population by one and changing the

1048 mean and variance of the trait distribution.

1049   This rule is derived from the equation of the regression line in a parent-offspring

1050 regression (DeLong & Belmaker 2019). To verify that the realization of this rule in a GEM

1051 implementation generates a parent-offspring regression with an estimated h^2 that matches

1052 what was set in the model, we track parent and offspring traits through GEMs initialized with

1053 different h^2 values (0.9, 0.7, 0.5, and 0.3). Using simple linear regression of offspring traits on

1054 parent traits, we verify that the estimated h^2 (the slope of the regression) remains close to the

1055 expected h^2 (Fig. S1-S4).

30

1056   Over any short interval of time in a GEM run, the realized parent-offspring relationship

1057   behaves as expected. After accumulating observations over longer runs, however, we see that

1058   the h^2 appears to converge on one. This is also expected: as the population evolves, the parent

1059   and offspring traits move in phenotypic space (as you can see from the changing x- and y-axis

1060   ranges in Figs. S1-S4), "smearing" the parent-offspring regressions (each of which has a slope of

1061 h^2 at any one moment in time) into a parent-offspring regression that has a slope approaching
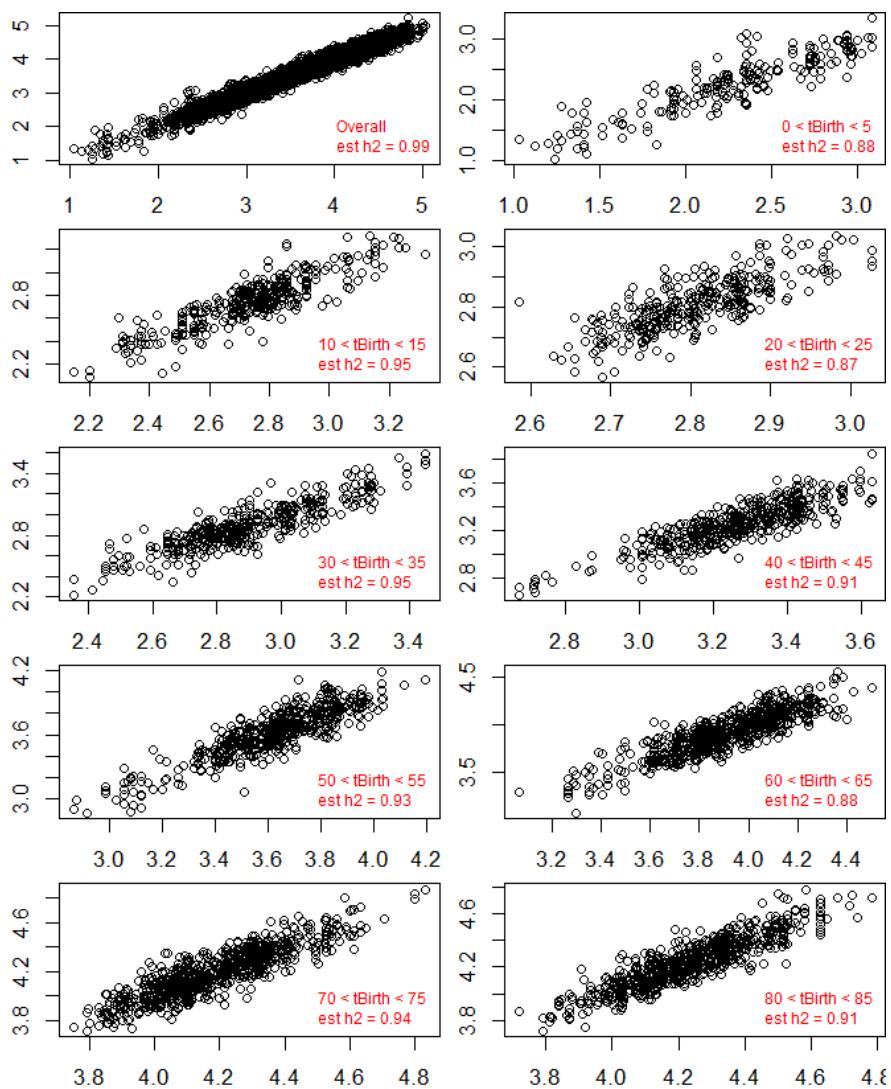
1062   one.

1063
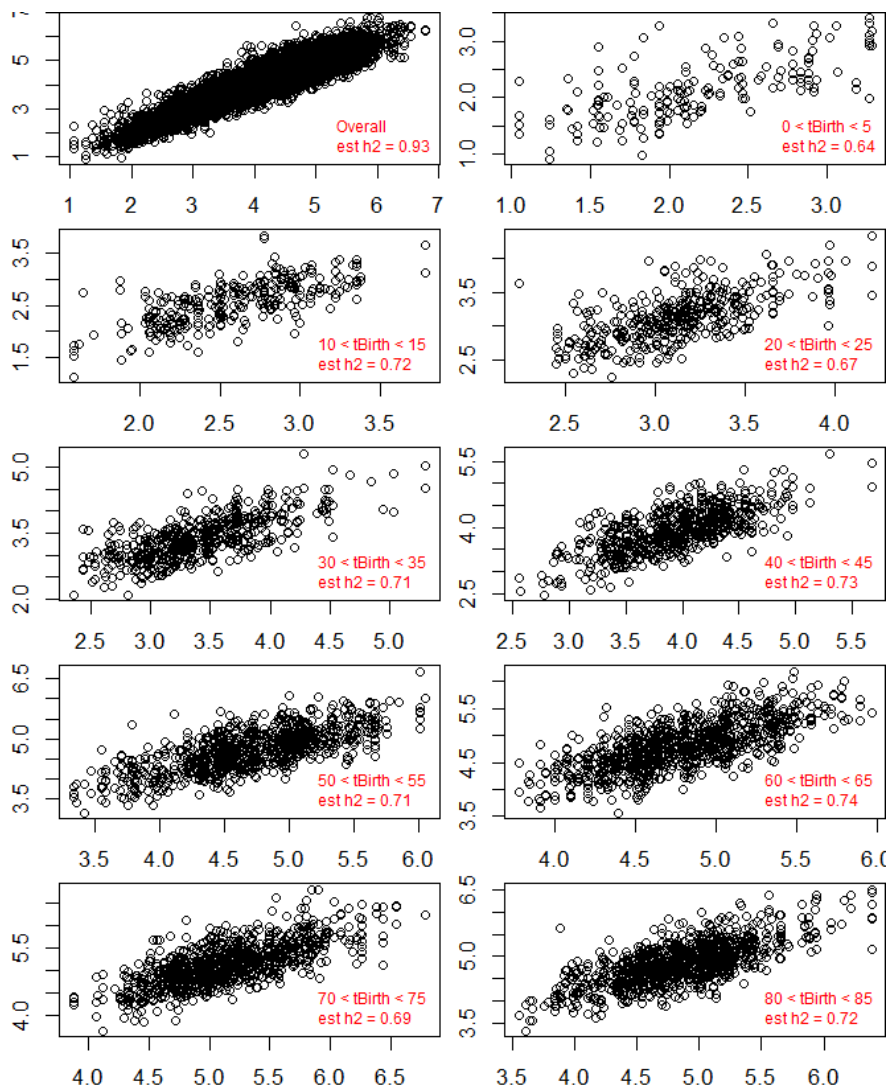1064   Fig. S1. Parent-offspring regressions through time when h^2 = 0.9.
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1070   Fig. S2. Parent-offspring regressions through time when h^2 = 0.7.
1071
1072
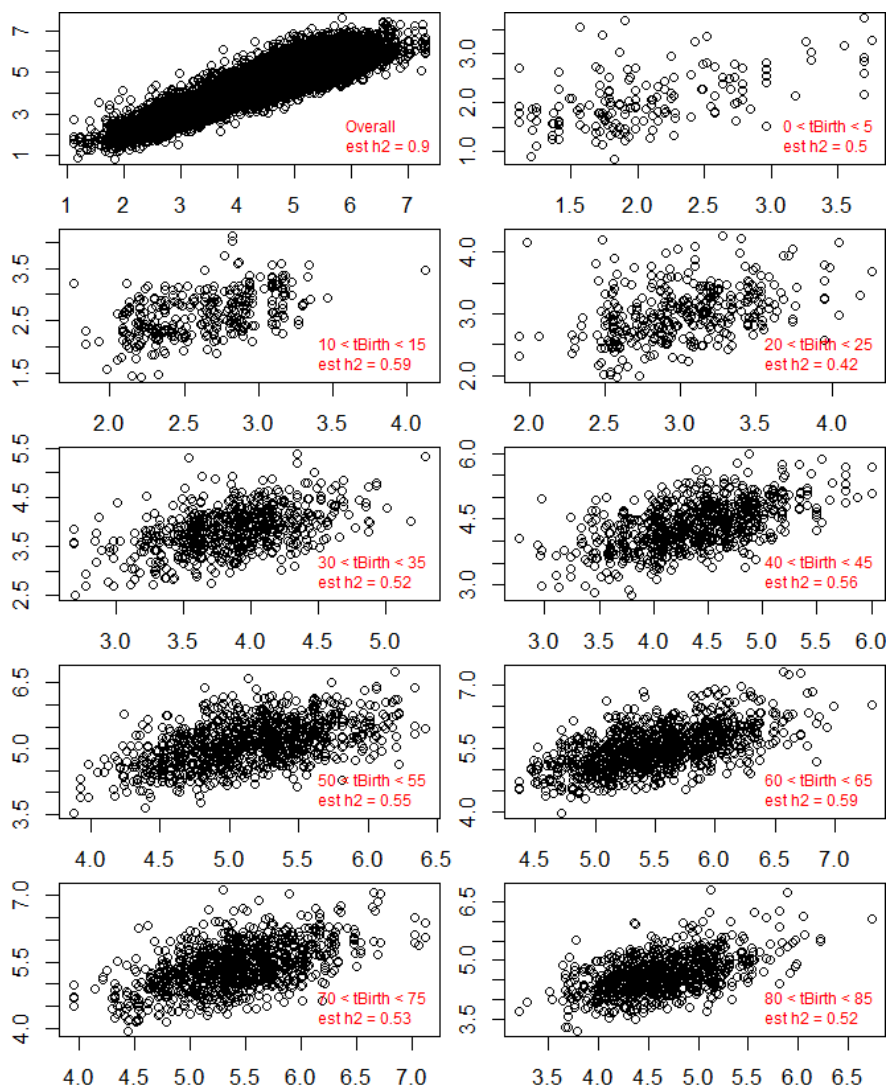
1073
1074
1075   Fig. S3. Parent-offspring regressions through time when h^2 = 0.5.
1076
1077

Overall
est h2 = 0.82

0 < tBirth < 5
est h2 = 0.22

10 < tBirth < 15
est h2 = 0.38

20 < tBirth < 25
est h2 = 0.33

30 < tBirth < 35
est h2 = 0.38

40 < tBirth < 45
est h2 = 0.32

50 < tBirth < 55
est h2 = 0.31

60 < tBirth < 65
est h2 = 0.3

70 < tBirth < 75
est h2 = 0.39

80 < tBirth < 85
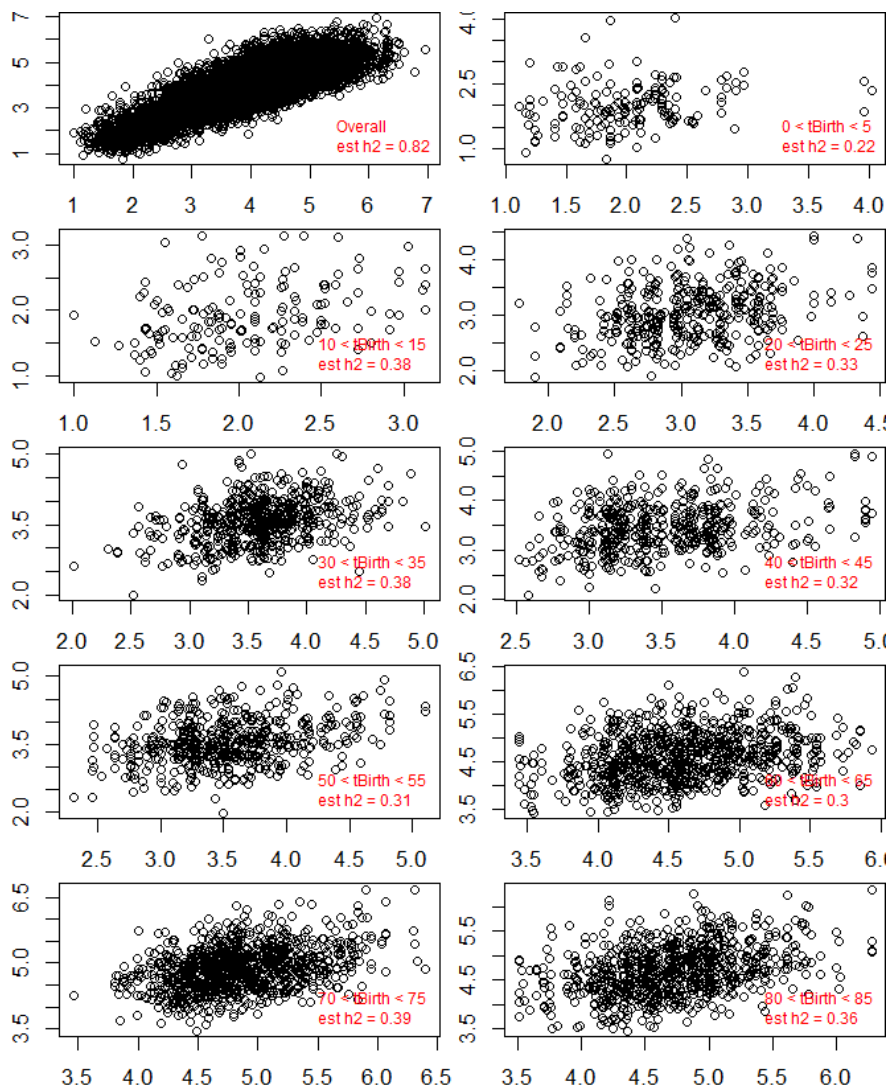est h2 = 0.36

1078
1079
1080   Fig. S4. Parent-offspring regressions through time when h^2 = 0.3.
1081

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