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E-Article

Snared in an Evil Time: How Age-Dependent Environmental and Demographic Variability Contribute to Variance in Lifetime Outcomes

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ABSTRACT: To what degree is lifetime success determined by innate individual quality versus external events and random chance, whether success is measured by lifetime reproductive output, life span, years that a tree spends in the canopy, or some other measure? And how do external events and chance interact with development (survival and growth) to drive success? To answer these questions, we extend our earlier age partitioning of luck in lifetime outcomes in two ways: we incorporate effects of external environmental variation, and we subdivide demographic luck into contributions from survival and growth. Applying our methods to four case studies, we find that luck in survival, in growth, or in environmental variation can all be the dominant driver of success, depending on life history, but variation in individual quality remains a lesser driver. Luck in its various forms is most important at very early ages and again close to the time when individuals typically first begin to be successful (e.g., entering the canopy, reaching reproductive maturity), but different forms of luck peak at different times. For example, a favorable year can boost a tree into the canopy, while luck in survival is required to take full advantage of that fortunate event.

Keywords: reproductive skew, lifetime reproductive success, trait variation, individual heterogeneity, individual stochasticity, environmental variation.

> Man mai longe lives weene
> ac him lighet oft the wrench;
> vair weder oft went into reene
> veerlich maket hit his blench.
>
> ("Man may expect long life but
> the trick often deceives him;
> fair weather often turns into
> rain—suddenly it plays its trick";
> thirteenth-century English song)

Introduction

How much is success driven by individual quality, how much by external factors, and how much by random chance?

Two identical individuals will not lead identical lives, even in identical circumstances. In a given year, one is likely to grow a little more than the other, to have more offspring than the other, to die before the other. Of course, individuals are not identical. They differ in their traits and other fixed attributes. Nonetheless, we and others have shown that in constant identical environments, luck in survival/growth/reproduction has substantially more influence on lifetime measures of success such as life span or lifetime reproductive output than differences in traits (Tuljapurkar et al. 2009; Steiner et al. 2010; Caswell 2011; Steiner and Tuljapurkar 2012; van Daalen and Caswell 2017; Hartemink and Caswell 2018; Jenouvrier et al. 2018*b*; Snyder and Ellner 2018; Broekman et al. 2020; Snyder et al. 2021).[1]

But researchers have not been able to evaluate how strongly external factors influence success: how much does environmental variation drive variation in success? Van Daalen and Caswell (2020) analyze the effects of a stochastically varying fire environment, but in their analysis the contribution of environmental variation was limited to the effect of the environment state when an individual is born, while effects of subsequent environmental variation are combined with luck in demographic transitions. One of the goals of this

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[1] What we have called luck and traits, Caswell and collaborators have called individual stochasticity and heterogeneity, while Tuljapurkar and collaborators refer to them as dynamic heterogeneity and fixed individual differences.

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article is to study how much the variance in measures of lifetime success is inflated by ongoing environmental variation. Does environmental variation influence success as much as other forms of luck, or is it more like trait variation, a lesser determinant? Moreover, we would like know how environmental variation interacts with development: when in an individual's life is it most important to get a good year? Are there generic vulnerable periods in an individual's life when it is important to be lucky in both demographic transitions and environmental conditions, or are the critical periods for environmental luck and demographic luck different?

A second goal of this article is to dissect more finely the sources of demographic luck. We previously found that state trajectory luck—the result of taking different paths through life—is typically the dominant source of variance in lifetime reproductive output (Snyder and Ellner 2018; Snyder et al. 2021). But is this large influence driven mainly by variance in the length of that life or by the variation in state transitions (e.g., growth) during that life? Here, in addition to quantifying the effect of environmental variation, we partition state trajectory luck into contributions from survival and from transitions between states.

In this article, we build on the mathematical approach in Snyder et al. (2021) to derive a partitioning of the variance of individual lifetime success into contributions from fixed trait variation, four forms of demographic luck (birth state luck, fecundity luck, survival trajectory luck, and growth trajectory luck), and two kinds of environmental luck (birth environment luck and environment trajectory luck). Each of these contributions is further partitioned into contributions at different ages.

Figure 1 shows a conceptual illustration of the different kinds of luck, while table 1 gives examples of each. Birth state luck measures how much variation in individual state at birth contributes to variance in lifetime success—for example, those born larger or earlier in the year may have an advantage. Fecundity luck quantifies how much random variation in number of offspring at a given age affects

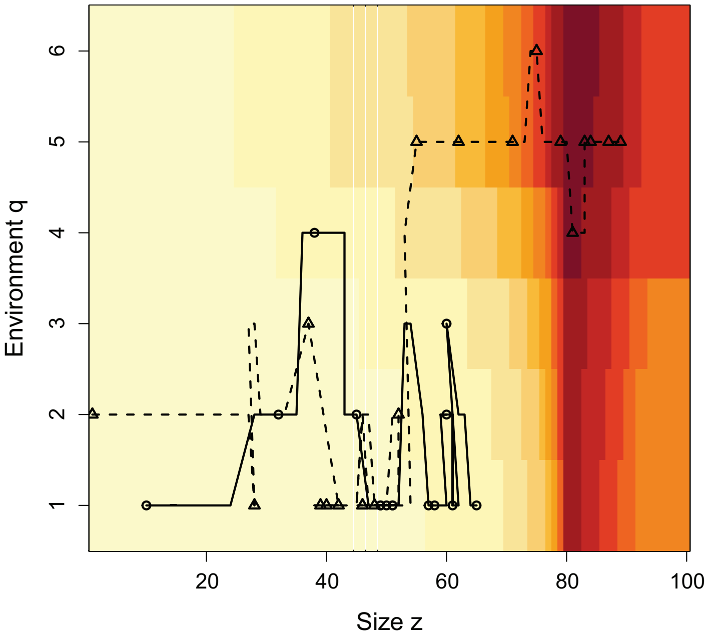

Figure 1: Conceptual figure showing how different forms of luck contribute to variance in lifetime success. The x-axis represents different values of the individual state z, which in this example is individual size, while the y-axis represents different environment state values q: every (z, q) represents a potential state in the megamatrix system. The two black lines represent two life trajectories, with one individual starting at size 10 in environment 1 and the other individual starting at size 1 in environment 2. Circles or triangles are placed every 5 years to help visualize the speed of growth. In this example, individuals mostly grow or stay the same size, so the trajectories proceed mostly rightward or vertically. The color in the heat map is expected total future success: individuals of size $z \approx 80$ have the best future prospects. Individuals younger and smaller or older and larger have either lower annual fecundity or lower survival. Birth state luck is the variation that comes from initial z value, while birth environment luck is the variation in lifetime success that comes from variation in initial q value. Survival trajectory luck at a given age is the variation that comes from having your life terminate or continue to the next time step, growth trajectory luck at a given age is the variation that comes from moving left or right in the next step, and environment trajectory luck is the variation that comes from moving up or down in the next step—these turns in the path take individuals through redder and less red areas. We have not shown offspring production or other annual success in this schematic, but fecundity luck at a given age is the variation that comes from how much success an individual accrues at that age.

Table 1: The different types of luck, with examples of good luck and its consequences

Luck type	Example	Consequence
Birth state luck	Large birth size	Spend less time at small sizes, which often experience high mortality
Birth environment luck	Born in a year with adequate rain	Higher survival and faster growth
Survival trajectory luck	Did not die this year	Might eventually reach minimum size for reproduction
Growth trajectory luck	Transitioned to a size or stage with low mortality rate	More likely to eventually reach minimum size for reproduction
Environment trajectory luck	A forest gap opened up in the adjacent site	The extra light allows higher growth and survival until it closes
Fecundity luck	Successfully reared twins	Larger than average annual increment in lifetime reproductive output

variance in lifetime reproductive output. If our measure of lifetime success is some other sum of successes over time, then fecundity luck arises more generally from random variation in that yearly measure at each age. Survival trajectory luck summarizes how survival at a given age affects variance in lifetime success,[2] while growth trajectory luck does the same for growth at a given age (or transitions between states if the model is not structured by size). Survival and growth trajectory luck sum to what we have previously called state trajectory luck. Birth environment luck specifies how much random variation in the birth year environment contributes to variance in lifetime success: for example, was a seedling born into a high-light environment or a low-light one? Environment trajectory luck at a given age quantifies how much random variation in the environment at that age affects variance in lifetime success. And finally, the contribution of fixed trait variation, which we have sometimes called "pluck" (Snyder and Ellner 2018), measures how fixed differences between individuals—genotype, birth date, mother's weight, the location of a sessile individual, a fixed behavioral syndrome—contribute to variance in lifetime success.

We demonstrate our new methods with four contrasting empirical case studies. The contribution of survival trajectory luck dominates in our first case study, a model of two tropical trees, *Simarouba amara* and *Minquartia guianensis*, experiencing varying light levels (Metcalf et al. 2009). By contrast, growth trajectory luck contributes more than survival trajectory luck except at very early ages in our second case study, a model of the desert shrub *Artemisia ordosica* (Li et al. 2011). (We do not have information on environment variation for this species.) In our third case study, a model of a fire-adapted perennial, *Lomatium bradshawii* (Kaye and Pyke 2003), the contribution of environment trajectory luck is dominant except at very early ages. Finally, we analyze a model with trait-dependent demographic variation that depends on environmental conditions: fulmars (*Fulmarus glacioides*) experience varying sea ice levels and are characterized by fixed behavioral syndromes that determine their survival and reproductive rates (Jenouvrier et al., forthcoming).

Peaks in luck terms tend to occur at or shortly after birth (there will be no success if you die young) and again close to the time individuals are typically first successful (when a little luck can push an individual over a size threshold or into a breeding class for the first time). In many cases, initial contributions to the variance of the success measure come soon enough after birth that we get a cluster of peaks at young ages; however, for the trees there is a distinct second set of peaks as they approach the canopy.

Peaks in the contributions of survival, growth, and environment luck can occur at different ages. One form of luck may be most important in avoiding an early death, while another form may be most important in getting past the threshold of success. Or in the case of the trees, the contributions of all forms of luck peak at birth or shortly thereafter, but the secondary peaks occur at different ages—getting a favorable environment can push you into the canopy, while once you are there, survival luck becomes important so that you can take advantage of it. While there are likely to be generically vulnerable periods (at or near birth), there can also be distinct periods of life when getting a favorable environment, a growth spurt, or luck in survival is especially important. As expected, increasing positive temporal autocorrelation of environmental conditions increases the importance of birth environment luck and environment trajectory luck—encountering good or bad conditions is more important if those conditions usually persist for a substantial fraction of a life span.

It is important to be clear about exactly what variance we are analyzing: it is the variance in success among a cohort of individuals that each experience their own sequence of environment states, independent of others. This is the scenario described by so-called megamatrix models for individuals in a Markovian time-varying environment (e.g., Pascarella and Horvitz 1998; Tuljapurkar and Horvitz 2006; van Daalen and Caswell 2020). It is most reasonable

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[2] The concept of survival trajectory luck was anticipated by Terry Pratchett, among others: the lion "had lived in the desert for sixteen years, and the reason it had lived so long was that it had not died" (Pratchett 1992).

if the environment varies spatiotemporally at a fine spatial scale, such as conspecific trees in a tropical forest that each experience their own sequence of light environments determined mainly by close neighbors (Metcalf et al. 2009). Studying a fire-adapted herbaceous perennial plant in Florida rosemary scrub, Coutts et al. (2021) similarly found that fine-scale (<10-m) spatial variation in expected lifetime reproductive success was as large as the temporal variation in success imposed by fires, with large variation both within and between gaps (the open sandy areas between shrubs, where the species grows). Alternatively, the megamatrix scenario can be thought of as replicating (if we could) one individual's partially random path through life over and over again and looking at the variation among replicate simulations.

A remaining challenge is to compute the contribution of temporal environmental variation to the outcome variation among a cohort of individuals that all experience the same random sequence of environment states. Intuitively, we would expect this contribution to be small because environments experienced in common do not intrinsically create differences between individuals—it can even be negative in theory, decreasing the variance in lifetime outcomes. The independent environments scenario that we consider here gives environmental variation the greatest opportunity to contribute substantially to among-individual variance in lifetime outcomes.

At the population level, average success is what drives population and evolutionary dynamics: in a sufficiently large population, individual-level luck averages out and traits that improve expected fitness increase in frequency (Snyder and Ellner 2018). However, in finite populations (and all populations are finite), highly skewed offspring distributions among genetically identical individuals can have substantial quantitative effects on evolutionary dynamics, including the fixation probability of new beneficial mutations and the site frequency spectra of neutral alleles (Okada and Hallatschek 2021). And for each individual, what happens in its own life is typically dominated by luck.

Model and Assumptions

We consider a structured population model in which there is dynamic variation in individual stage or state (often variation in size), fixed trait variation among individuals, and environmental variation. The joint state and environment dynamics for any individual are assumed to be governed by a stationary Markov chain—that is, a discrete-time stochastic process with the Markov property and time-invariant transition probabilities. The set of possible state and environment values may be continuous (i.e., an integral projection model [IPM]), discrete (i.e., a matrix projection model [MPM]), or mixed. A stationary Markov chain is always a linear operator on probability distributions, even if the transition probabilities are (for example) nonlinear functions of individual size or environment quality. However, a density-dependent MPM or IPM would not have stationary transition probabilities. Stationarity might hold because the underlying IPM or MPM is not density dependent or because the dynamics have been linearized about an equilibrium of the density-dependent dynamics.

The joint dynamics of individual stage/state and environment state (for any particular value of the fixed trait) can be modeled using a so-called transition megamatrix in which individuals are cross classified by individual and environment states.[3] Let R be a random variable representing lifetime success—lifetime reproductive output, life span, number of years in the canopy, and so on. We would like to determine how much of $\mathrm{Var}(R)$ is due to environmental variation (or any other dynamic trait with Markovian dynamics), how much is due to various forms of demographic luck, and how much is due to fixed trait variation and to further partition each of these into contributions at different ages.

Notation. Our notation is described in table 2 as well as in the text. We let q_a be the environment state ("quality") at age a and let z_a be the individual state at age a, either a discrete stage or a continuous variable such as size. One possible state is ω (dead). Note that indexing by age (q_a, z_a) is the same as indexing by time (q_t, z_t) if we are modeling an individual, although not if we are modeling a population. We assume that the dead have no current or future reproduction. We let x denote a fixed trait (or trait vector) that varies among individuals—some models will have this feature, others will not. The state transition and environment transition probabilities can both depend on x.

We assume that at time t, each individual's current environment determines its transition probabilities from state z_t to z_{t+1}, and then the environment is updated from q_t to q_{t+1}. The term q_t represents the state of external conditions between the t and $t+1$ censuses at which we measure individual state. The terms q_t and z_t jointly and fully determine the probability distribution for immediate reproductive success (i.e., the number of new offspring produced between t and $t+1$ that recruit into the population at time $t+1$). That is, given q_t and z_t, immediate reproductive success is independent of q and z at all other times, past and future. These timing conventions are depicted in figure 2. Environment state affects individual state transitions, but we assume that the reverse is not true: the conditional distribution of q_{t+1} given q_t and z_{t+1} equals the conditional distribution given just q_t.

As noted in the introduction, our calculations assume that the environmental state draw is specific to the individual, so that the variance in lifetime outcomes across replicate random simulations of one individual's life is equivalent to

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[3] In IPM terminology, this is an example of a size-quality model.

Table 2: Notation and definitions

Notation	Formula and/or meaning
$c_0(z)$	Probability distribution of state (or state and trait) at birth; $c_0(\omega) = c_0(\omega, \bullet) = 0$; individuals are age 0 at birth
$\mathbf{e}$	Vector of all 1s (MPM) or function $\mathbf{e}(z) \equiv 1$ (IPM); in both cases, $\mathbf{e}^{\mathsf{T}}P =$ state-specific survival probability
F	Fecundity kernel
$G_\bullet$	Megamatrix-sized block diagonal matrix that updates state conditional on survival but not environment
G_q	Growth kernel/matrix conditional on environment q
M	Megamatrix governing joint transitions of state and environment
$m_0(z, q)$	Megamatrix probability distribution of state and environment (or state and environment and trait) at birth
N	Fundamental matrix for P: $N = (I - P)^{-1}$
ω	Dead; an absorbing state (the dead stay dead) with zero fecundity
P	Survival-growth kernel or matrix without an absorbing state for death; thus, $\mathbf{e}^{\mathsf{T}}P = s(z)$, state-dependent survival
$P_\bullet$	Megamatrix-sized block diagonal matrix that updates state but not environment
$p_0(x)$	Marginal distribution of trait at birth
Q	Environment transition kernel or matrix
q, q_a	Possible value of individual environment or environment at age a
R	Lifetime success, a random variable (e.g., lifetime reproductive output)
$\rho_1(z, q)$	$\mathbb{E}$[immediate and future reproductive output] for state z, environment q individual
$\rho_1'(z', q)$	The conditional expectation of reproduction at ages $a + 1$ and beyond, as a function of the value of z'_{a+1}: $\mathbb{E}(\rho_1(z_{a+1}, q_{a+1}) \mid z'_{a+1} = z', q_a = q)$
$\rho_1^\circ(z, q)$	The conditional expectation of reproduction at $a + 1$ and beyond: $\mathbb{E}(\rho_1(z_{a+1}, q_{a+1}) \mid z_{a+1} = z, q_a = q)$
$S_\bullet$	Megamatrix-sized block diagonal matrix that updates survival but not growth or environment
S_q	Survival kernel/matrix conditional on environment q
$\sigma^2(z)$	Var(immediate success) for state z individual (formula is model dependent)
$u_0(q)$	Probability distribution of environment at birth
$V_e(z)$	Variance over next year's environment of $\rho_1(z)$
$V_g(z)$	Variance over next year's state of $\rho_1^\circ(z)$
$V_s(z)$	Variance over the next intermediate state of $\rho_1'(z)$
vec	Operator converting a matrix to a column vector by stacking its columns with the first column at the top, the second below it, and so on
x	Possible value of trait
$y_{j:k}$	The vector $(y_j, y_{j+1}, \dots, y_k)$; for example, $\mathbf{z}_{0:a}$ is an individual's history of states from ages 0 to a, considered as a random vector
z, z_a	Possible value of individual state or state at age a
$\mathbf{z}$, $\mathbf{z}_a$, $\mathbf{q}$, $\mathbf{q}_a$	Individual state or environment (or state or environment at age a) considered as a random variable

Note: Many of these can depend on trait x in addition to other variables, but for clarity we omit x dependence in those cases. P here corresponds to $\mathbf{U}$ in van Daalen and Caswell (2017), and ρ_1 here corresponds to $\bar{r}$ in Ellner et al. (2016).

the variance in outcomes across many replicate individuals having the same traits, initial state z_0, and environment state q_0.

In the remainder of this section, we work out in detail how to do the partitioning of variance in success described in the introduction. Readers who prefer to skip the technical details can find the recipes for calculating each term in equation (7) (fixed trait variation), equation (9) (birth state luck), equation (11) (birth environment luck), equation (S5) (state trajectory luck), equation (21) (environmental luck), and equation (23) (fecundity luck).

Variance Decomposition with Environmental Variation

Our decomposition of the variance of success follows the general variance decomposition in Bowsher and Swain (2012). For a statement and proof of the decomposition in terms of random variables (rather than the original σ-fields), see section S2 of the supplemental PDF for Snyder et al. (2021).

The basic idea behind this decomposition is to calculate the mean difference in outcome variance conditional on different amounts of information. For example, the mean difference between the variance conditioned on the state and environmental histories up to age a, averaged over those histories, and the (smaller) variance conditioned on those histories *and* the state at age $a + 1$, averaged over those histories, measures how much the randomness in the state transition between a and $a + 1$ contributes to the total variance in outcomes. Each term in the variance partitions below (eqq. (1)–(4)) equals one such difference in expected variance, even though it is not written in that form (see eq. [15] in Bowsher and Swain [2012] or eqq. [S10]–[S12] in Snyder et al. [2021]).

In principle, conditioning on multiple variables (e.g., states at multiple ages) can be done in any order, and the choice affects the resulting variance partition. However, the temporal order of events provides a natural sequence

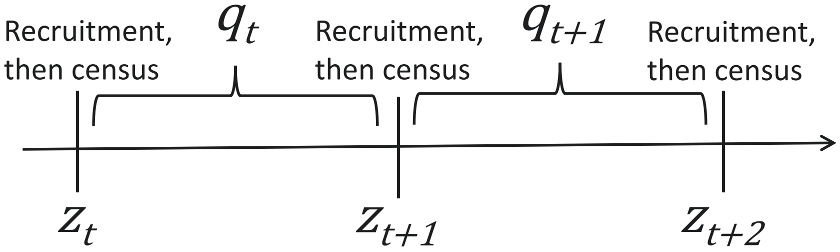

Figure 2: Assumed relationship between environment q_t and state z_t for decomposing variance in success with respect to environment and state transitions separately. Environment q_t affects transition probabilities from z_t to z_{t+1} and the current reproductive success at time t (i.e., the number of offspring that join the population as new recruits at time $t + 1$). Thus, the distribution of offspring recorded as new recruits at time $t + 1$ depends on z_t and q_t.

for partitioning luck by age: variances across later events are conditioned on earlier events. Here, we assume that each time step is broken up into a state transition (z_t to z_{t+1}) with transition probabilities depending on the environment state q_t, followed by an environment transition (q_t to q_{t+1}), as shown in figure 2. Thus, the variance of future reproductive output across possible states z_{a+1} is conditioned on individual state and environment at age a, while the variance over possible environments q_{a+1} is additionally conditioned on z_{a+1}. The same approach will still hold if the reverse temporal order is assumed for state and environment transitions, but one would need to rederive equations like those below that align with that ordering.

Applying the Bowsher and Swain (2012) general variance decomposition to our model gives

$$\begin{aligned}
\mathrm{Var}(R) = {} & \underbrace{\mathrm{Var}_{\mathbf{x}}[\mathbb{E}(R|\mathbf{x})]}_{\text{fixed trait variation (“pluck”)}} \\
& + \underbrace{\mathbb{E}_{\mathbf{x}}\{\mathrm{Var}_{\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0)]\}}_{\text{birth state luck}} \\
& + \underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}_0}\{\mathrm{Var}_{\mathbf{q}_0|\mathbf{x},\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0,\mathbf{q}_0)]\}}_{\text{birth environment luck}} \\
& + \underbrace{\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}_{0:a},\mathbf{q}_{0:a}}\{\mathrm{Var}_{z_{a+1}|\mathbf{x},\mathbf{z}_{0:a},\mathbf{q}_{0:a}}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a})]\}}_{\text{state trajectory luck}} \\
& + \underbrace{\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a}}\{\mathrm{Var}_{\mathbf{q}_{a+1}|\mathbf{x},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a}}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a+1})]\}}_{\text{environmental trajectory luck}} \\
& + \underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}_{0:A},\mathbf{q}_{0:A}}\mathrm{Var}[R|\mathbf{x},\mathbf{z}_{0:A},\mathbf{q}_{0:A}]}_{\text{fecundity luck}}\,.
\end{aligned}\tag{1}$$

Before going any further, we simplify equation (1). Environment transitions are Markov and unaffected by state transitions, and state transition probabilities from a to $a + 1$ depend only on z_a and q_a. We therefore have

$$\begin{aligned}
\mathrm{Var}(R) = {} & \underbrace{\mathrm{Var}_{\mathbf{x}}[\mathbb{E}(R|\mathbf{x})]}_{\text{fixed trait variation (“pluck”)}} \\
& + \underbrace{\mathbb{E}_{\mathbf{x}}\{\mathrm{Var}_{\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0)]\}}_{\text{birth state luck}} \\
& + \underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}_0}\{\mathrm{Var}_{\mathbf{q}_0|\mathbf{x},\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0,\mathbf{q}_0)]\}}_{\text{birth environment luck}} \\
& + \underbrace{\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}_a,\mathbf{q}_a}\{\mathrm{Var}_{\mathbf{z}_{a+1}|\mathbf{x},\mathbf{z}_a,\mathbf{q}_a}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_{a+1},\mathbf{q}_a)]\}}_{\text{state trajectory luck}} \\
& + \underbrace{\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}_{a+1},\mathbf{q}_a}\{\mathrm{Var}_{\mathbf{q}_{a+1}|\mathbf{x},\mathbf{q}_a}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_{a+1},\mathbf{q}_{a+1})]\}}_{\text{environment trajectory luck}} \\
& + \underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}_{0:A},\mathbf{q}_{0:A}}\mathrm{Var}[R|\mathbf{x},\mathbf{z}_{0:A},\mathbf{q}_{0:A}]}_{\text{fecundity luck}}\,.
\end{aligned}\tag{2}$$

The term called “prenatal luck” in our previous decomposition without environmental variation (Snyder et al. 2021) is split here into birth state luck and birth environment luck. Similarly, there are two kinds of luck due to transitions at each age: state trajectory luck coming from z transitions, and environmental variation coming from q transitions.

Partitioning State Trajectory Luck into Survival and Growth Components

In previous articles, our interpretation of patterns in the importance of luck has often invoked the idea that the contribution of luck in general and state trajectory luck in particular peaks at ages, stages, or states where it is especially important not to die. However, those interpretations were based on an intuition that the dichotomy of survival versus death is overshadowing everything else. But is that really true, or can variability in growth (given survival) also be important and perhaps sometimes dominate the importance of survival?

In this section, we provide a way to answer that question and to confirm or refute our previous interpretations by decomposing state trajectory luck at each age into contributions from survival and growth. To do that, we break each time step into three events, as shown in figure 3. First, do you survive to the next census or not? Second, conditional on surviving, what is your state at the next census? Third, what is your next environment state?

The term z'_{t+1} denotes the state after possible mortality; this equals z_t if the individual survives and ω if the individual dies. The diagram assumes that mortality precedes growth between one census and the next, but this is not really an assumption. For any sequence of events or if mortality and growth are ongoing throughout the time step, we can express the outcome distribution $P_q(z', z)$ as the product of the survival probability $s_q(z) = \int P_q(z', z)\,dz'$ with conditional growth distribution $G_q(z', z) = P_q(z', z)/s_q(z)$.

For the sequence of events in figure 3, the Bowsher and Swain decomposition then says that $\mathrm{Var}(R)$ equals

$$
\begin{aligned}
&\underbrace{\mathrm{Var}_{\mathbf{x}}[\mathbb{E}(R|\mathbf{x})]}_{\substack{\text{trait variation}\\ \text{(“pluck”)}}}\\
&+\underbrace{\mathbb{E}_{\mathbf{x}}\{\mathrm{Var}_{\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0)]\}}_{\text{birth state luck}}\\
&+\underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}_0}\{\mathrm{Var}_{\mathbf{q}_0|\mathbf{x},\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0,\mathbf{q}_0)]\}}_{\text{birth environment luck}}\\
&+\underbrace{\begin{array}{l}\displaystyle\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}'_{0:a},\mathbf{z}_{0:a},\mathbf{q}_{0:a}}\{\mathrm{Var}_{\mathbf{z}'_{a+1}|\mathbf{x},\mathbf{z}'_{0:a},\mathbf{z}_{0:a},\mathbf{q}_{0:a}}\\ \qquad\qquad[\mathbb{E}(R|\mathbf{x},\mathbf{z}'_{0:a+1},\mathbf{z}_{0:a},\mathbf{q}_{0:a})]\}\end{array}}_{\text{survival trajectory luck}}\\
&+\underbrace{\begin{array}{l}\displaystyle\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}'_{0:a+1},\mathbf{z}_{0:a},\mathbf{q}_{0:a}}\{\mathrm{Var}_{\mathbf{z}_{a+1}|\mathbf{x},\mathbf{z}'_{0:a+1},\mathbf{z}_{0:a},\mathbf{q}_{0:a}}\\ \qquad\qquad[\mathbb{E}(R|\mathbf{x},\mathbf{z}'_{0:a+1},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a})]\}\end{array}}_{\text{growth trajectory luck}}\\
&+\underbrace{\begin{array}{l}\displaystyle\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}'_{0:a+1},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a}}\{\mathrm{Var}_{\mathbf{q}_{a+1}|\mathbf{x},\mathbf{z}'_{0:a+1},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a}}\\ \qquad\qquad[\mathbb{E}(R|\mathbf{x},\mathbf{z}'_{0:a+1},\mathbf{z}_{0:a+1},\mathbf{q}_{0:a+1})]\}\end{array}}_{\text{environmental trajectory luck}}\\
&+\underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}'_{0:A},\mathbf{z}_{0:A},\mathbf{q}_{0:A}}\mathrm{Var}[R|\mathbf{x},\mathbf{z}'_{0:A},\mathbf{z}_{0:A},\mathbf{q}_{0:A}]}_{\text{fecundity luck}}\,.
\end{aligned}
\tag{3}
$$

We now simplify. All transitions are Markovian, and fecundity at age a is fully determined by (z_a, q_a). The age decomposition is then

$$
\begin{aligned}
&\underbrace{\mathrm{Var}_{\mathbf{x}}[\mathbb{E}(R|\mathbf{x})]}_{\substack{\text{trait variation}\\ \text{(“pluck”)}}}\\
&+\underbrace{\mathbb{E}_{\mathbf{x}}\{\mathrm{Var}_{\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0)]\}}_{\text{birth state luck}}\\
&+\underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}_0}\{\mathrm{Var}_{\mathbf{q}_0|\mathbf{x},\mathbf{z}_0}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_0,\mathbf{q}_0)]\}}_{\text{birth environment luck}}\\
&+\underbrace{\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}_a,\mathbf{q}_a}\{\mathrm{Var}_{\mathbf{z}'_{a+1}|\mathbf{x},\mathbf{z}_a,\mathbf{q}_a}[\mathbb{E}(R|\mathbf{x},\mathbf{z}'_{a+1},\mathbf{q}_a)]\}}_{\text{survival trajectory luck}}\\
&+\underbrace{\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}'_{a+1},\mathbf{q}_a}\{\mathrm{Var}_{\mathbf{z}_{a+1}|\mathbf{x},\mathbf{z}'_{a+1},\mathbf{q}_a}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_{a+1},\mathbf{q}_a)]\}}_{\text{growth trajectory luck}}\\
&+\underbrace{\sum_{a=0}^{A-1}\mathbb{E}_{\mathbf{x},\mathbf{z}_{a+1},\mathbf{q}_a}\{\mathrm{Var}_{\mathbf{q}_{a+1}|\mathbf{x},\mathbf{q}_a}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_{a+1},\mathbf{q}_{a+1})]\}}_{\text{environment trajectory luck}}\\
&+\underbrace{\mathbb{E}_{\mathbf{x},\mathbf{z}_{0:A},\mathbf{q}_{0:A}}\mathrm{Var}[R|\mathbf{x},\mathbf{z}_{0:A},\mathbf{q}_{0:A}]}_{\text{fecundity luck}}\,.
\end{aligned}
\tag{4}
$$

Comparing this to the decomposition (2), we see that state trajectory luck has been replaced by two separate terms for survival trajectory luck and growth trajectory luck, and the other terms are all identical to the prior decomposition.

Computing the Terms

We now derive analytic formulas for each term in equation (4), following closely the corresponding section of our previous article. These formulas will imply (exactly as in Snyder et al. 2021) that we can let $A \to \infty$ in equation (4) to get a decomposition across all ages, so long as there is a number $s_{\max} < 1$ and time span τ such that every individual in any environment (any x, z, q values at time t) has probability at most $s_{\max}$ of surviving to time $t + \tau$.

Each term in equation (4) is a moment with respect to the distribution of x at birth, so the task at hand is to compute each integrand for any given x value. So until further notice, we suppress x dependence to simplify the notation. We use kernel notation to be fully explicit about the integrals/sums in analytic formulas, but we use matrix notation in calculation formulas because in practice those will be matrix operations even for IPMs. Those formulas

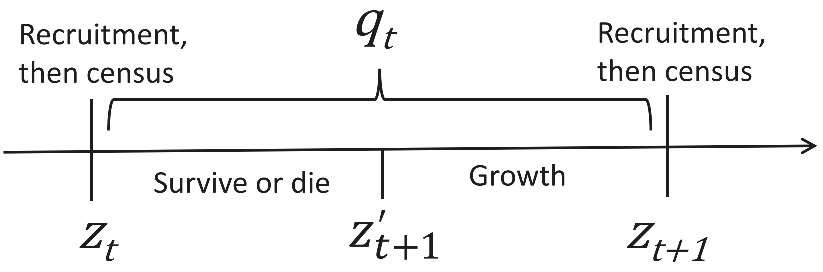

Figure 3: Assumed relationship between environment q_t and state transitions for further decomposing state trajectory luck into survival luck and growth luck. Environment q_t affects the chance of survival between t and $t+1$ (the z_t to z'_{t+1} transition), the growth conditional on survival (z'_{t+1} to z_{t+1}), and the current reproductive success at time t. So as before, the distribution of offspring recorded as new recruits at time $t+1$ is a function of z_t and q_t.

assume that the IPM has been implemented using a bin-to-bin method, such as the midpoint rule (see Ellner et al. 2016, ch. 6), so that on the computer it is equivalent to a large MPM. However, readers should be aware that in the latter case matrix notation may hide bin-width factors that are used in numerical integration; for example, $v^{\mathsf{T}}w$, denoting $\int v(x)w(x)\,dx$, would be calculated as `h · sum(v · w)` if `v` and `w` are vectors storing $v(x)$ and $w(x)$ values at integration mesh points and h is the distance between mesh points. Additionally, calculation formulas assume that the model (IPM or MPM) has been implemented as a size-quality model in the format of Ellner and Rees (2006, app. A) and Ellner et al. (2016, sec. 6.6.2), which is the same layout as a standard megamatrix MPM. That is, the state distribution $n(z, q, t)$ is represented as a matrix whose (i, j) entry is $n(z_i, q_j, t)$, the vec operator converts such matrices to vectors by stacking the columns with column 1 at the top, then column 2, and so on, and transition matrices are constructed to operate appropriately on those vectors (for full details and R code, see either of the references cited above).

Now we make some definitions. The term $P_q(z', z)$ is the transition matrix/kernel for states z in environment q. In the matrix case, $P_q(i, j)$ is the transition probability from state j to state i. The term $Q(q', q)$ is the transition matrix/kernel for environment states q. The term $M(z', q'|z, q)$ is the transition probability function governing joint state and environment transitions: $M(z', q'|z, q) = P_q(z', z) \times Q(q', q)$. The function $\rho_1(z, q) = \mathbb{E}(R|x, z_0 = z, q_0 = q)$, expected success (current and future) as a function of current state.[4]

Below, we tacitly assume that any function, vector, or matrix is restricted to living states—this differs from the notation in Snyder et al. (2021). The term $c_0(z)$ is the initial distribution for states, $u_0(q)$ is the initial distribution for environments, and $m_0(z, q) = c_0(z) \times u_0(q)$ is the initial cross-classified distribution. We assume that initial state and initial environment are independent. We do not assume that an individual's initial environment is drawn from the stationary distribution of the environment chain.

Let $N = (I - M)^{-1}$ be the fundamental matrix/operator associated with M and F be the fecundity megamatrix. Then as usual,

$$\operatorname{vec}(\rho_1) = \mathbf{e}^{\mathsf{T}} F N \tag{5}$$

gives expected current and future success as a function of (z, q) at a census time, where $\mathbf{e}$ is a vector of all 1s (MPM) or a constant function with value 1 (IPM).

The first three terms in equation (4) can all be calculated from ρ_1. For the first term, we have

$$\begin{aligned} \mathbb{E}(R) &= \iint \rho_1(z, q) m_0(z, q)\,dz\,dq \\ &= (\operatorname{vec}(\rho_1))^{\mathsf{T}} \operatorname{vec}(m_0). \end{aligned} \tag{6}$$

In models with a fixed trait x, both ρ_1 and m_0 can depend on x. The fixed trait variation term in equation (4) is the variance of $\mathbb{E}(R)$ as a function of x with respect to the trait distribution at birth, $p_0(x)$. Suppressing the dependence of m_0 and ρ_1 on z and q for notational clarity,

$$\begin{aligned} \text{fixed trait variation} &= \operatorname{Var}_{\mathbf{x}}[\mathbb{E}(R|\mathbf{x})] \\ &= \int \left((\operatorname{vec}(\rho_1(x)))^{\mathsf{T}} \operatorname{vec}(m_0(x))\right)^2 p_0(x)\,dx \\ &\quad - \left[\int ((\operatorname{vec}(\rho_1(x)))^{\mathsf{T}} \operatorname{vec}(m_0(x))) p_0(x)\,dx\right]^2. \end{aligned} \tag{7}$$

For the second term (birth state luck),

$$\mathbb{E}(R|z_0) = \int \rho_1(z_0, q) u_0(q)\,dq = \rho_1 u_0, \tag{8}$$

---

[4] Because of the Markovian dynamics, calculating expected current and future success starting at (z, q) is the same as calculating lifetime success when born into (z, q).

the last equality assuming that $\rho_1(z, q)$ is stored as a matrix and u_0 as a vector summing to 1. Birth state luck is the variance of $\mathbb{E}(R|z_0)$ with respect to c_0:

$$\begin{aligned} \text{birth state luck} &= \mathrm{Var}_{z_0}[\mathbb{E}(R|z_0)] \\ &= c_0^\top(\rho_1 u_0)^2 - (c_0^\top \rho_1 u_0)^2. \end{aligned} \tag{9}$$

For the third term (birth environment luck), $\mathbb{E}(R|z_0, q_0) = \rho_1(z_0, q_0)$. First we need the variance with respect to q_0 for each z_0, given by

$$\begin{aligned} \int \rho_1(z_0, q)^2 u_0(q)\, dq - \left(\int \rho_1(z_0, q) u_0(q)\, dq \right)^2 \\ = \rho_1^2 u_0 - (\rho_1 u_0)^2. \end{aligned} \tag{10}$$

This needs to be averaged over the marginal distribution of z_0:

$$\text{birth environment luck} = c_0^\top[\rho_1^2 u_0 - (\rho_1 u_0)^2]. \tag{11}$$

For the trajectory luck lines in equation (4), the age a terms in the sums involve variances of R, total lifetime reproduction, conditional on events prior to the census at age $a + 1$. As in Snyder et al. (2021), we can break R up into two pieces: reproduction up though age a, and reproduction at ages $a + 1$ and beyond. In these three lines, it is only the second piece that varies as a function of z'_{a+1} (survival trajectory), z_{a+1} (growth trajectory), or q_{a+1} (environment trajectory), conditional on events up through age a. Thus, the conditional variances in those lines are the variance of reproduction at ages $a + 1$ and beyond.

To compute these variances, we need to express expected success conditional on (z'_{a+1}, q_a), the state where we have updated survival but not growth or environment, or on (z_{a+1}, q_a), the state where we have updated survival and growth but not environment. To enable this, let $P_\bullet$ denote the megamatrix-sized block diagonal matrix in which the blocks are the state transition or iteration matrices P_q for environment states $q_1, q_2, \ldots$.[5] Let $S_\bullet$ be the megamatrix-sized block diagonal matrix in which the blocks are the survival matrices S_q for environment states $q_1, q_2, \ldots$ and similarly for $G_\bullet$. (Formally, $S_\bullet$ is the survival operator whose action on living states is mapping the state vector $n(z, q, t) \mapsto s(z, q)n(z, q, t)$, and $G_\bullet$ is the growth operator mapping $n(z, q, t) \mapsto \int G(z, z_0, q)n(z_0, q, t)\, dz_0$.)

For survival trajectory luck, we need to compute the variance of $\mathbb{E}(R|\mathbf{x}, \mathbf{z}'_{a+1}, \mathbf{q}_a)]$ with respect to the distribution of $\mathbf{z}'_{a+1}$ conditional on $\mathbf{x}$, $\mathbf{z}_a$, $\mathbf{q}_a$. Splitting R into reproduction up to age a and reproduction from $a + 1$ onward, this variance is the variance of the conditional expectation of reproduction at ages $a + 1$ and beyond, as a function of the value of z'_{a+1}. That conditional expectation is given by

$$\begin{aligned} \rho_1'(z', q) &:= \mathbb{E}(\rho_1(z_{a+1}, q_{a+1})|z'_{a+1} = z', q_a = q) \\ &= \int \rho_1(z, y) G_q(z, z') Q(y, q)\, dz\, dy. \end{aligned} \tag{12}$$

In matrix form, we can write $\mathrm{vec}(\rho_1') = \mathrm{vec}(\rho_1 Q)G_\bullet$.

Survival trajectory luck is the variance of ρ_1' across the distribution of z'_{a+1} conditional on the current state z_a and the current environment q_a:

$$\begin{aligned} V_s(z, q) = \int (\rho_1'(z', q))^2 S_q(z', z)\, dz' \\ - \left(\int \rho_1'(z', q) S_q(z', z)\, dz' \right)^2. \end{aligned} \tag{13}$$

Note that the integrals on the right-hand side do not need to include the dead state, ω, because $\rho_1'(\omega, q) \equiv 0$. Because the kernel on the right-hand side depends on q, values of V_s for each q need to be computed separately. A direct approach is to compute V_s as

$$\mathrm{vec}(V_s) = (\mathrm{vec}(\rho_1')^2)^\top S_\bullet - (\mathrm{vec}(\rho_1')^\top S_\bullet)^2. \tag{14}$$

We then need to average V_s over the distribution of (z_a, q_a), given by $M^a \mathrm{vec}(m_0)$. The age partition of survival trajectory luck is then

$$\sum_{a=0}^{A-1} (\mathrm{vec}(V_s))^\top M^a \mathrm{vec}(m_0). \tag{15}$$

For growth trajectory luck, we need to compute the variance of $\mathbb{E}(R|\mathbf{x}, \mathbf{z}_{a+1}, \mathbf{q}_a)$ with respect to the distribution of $\mathbf{z}_{a+1}$ conditional on $\mathbf{x}$, $\mathbf{z}'_{a+1}$, $\mathbf{q}_a$. As above, only reproduction at ages $a + 1$ and beyond contributes to that variance. The conditional expectation of reproduction at $a + 1$ and beyond is given by

$$\begin{aligned} \rho_1^\circ(z, q) &:= \mathbb{E}(\rho_1(z_{a+1}, q_{a+1})|z_{a+1} = z, q_a = q) \\ &= \int \rho_1(z, q') Q(q', q)\, dq'. \end{aligned} \tag{16}$$

In matrix form, we can write $\mathrm{vec}(\rho_1^\circ) = \rho_1 Q$.

Growth trajectory luck is the variance of $\rho_1^\circ(z_{a+1}, q_a)$ across the distribution of z_{a+1} conditional on the current intermediate state z' and the current environment q:

$$\begin{aligned} V_g(z', q) = \int (\rho_1^\circ(z, q))^2 G_q(z, z')\, dz \\ - \left(\int \rho_1^\circ(z, q) G_q(z, z')\, dz \right)^2. \end{aligned} \tag{17}$$

---

[5] $P_\bullet$ can be built easily as a sparse matrix using the bdiag function in the Matrix library in R (Bates and Maechler 2019).

We compute V_g as

$$\mathrm{vec}(V_g) = (\mathrm{vec}(\rho_1^{\circ})^2)^{\mathsf{T}} G_{\bullet} - (\mathrm{vec}(\rho_1^{\circ})^{\mathsf{T}} G_{\bullet})^2. \tag{18}$$

Here, we need to average V_g over the distribution of (z'_{a+1}, q_a), which is given by $S_{\bullet}M^a\mathrm{vec}(m_0)$ (as usual in these calculations, this is the distribution over only the living states because the contribution from ω is zero). The age partition of growth trajectory luck is then

$$\sum_{a=0}^{A-1} (\mathrm{vec}(V_g))^{\mathsf{T}} S_{\bullet}M^a\mathrm{vec}(m_0). \tag{19}$$

Those wishing to calculate state trajectory luck can either add the contributions of survival and growth trajectory luck or follow the calculation in section S1.1 of the supplemental PDF. To calculate survival and growth trajectory luck in the absence of environmental variation, see section S1.2 of the supplemental PDF.

The variance in the environment trajectory luck term in equation (2) is the variance of $\rho_1(z_{a+1}, q_{a+1})$, across the conditional distribution of q_{a+1} given q_a. That variance, as a function of z_{a+1} and q_a, is given by

$$\begin{aligned} V_e(z, q) &= \int \rho_1(z, q')^2 Q(q', q)\, dq' \\ &\quad - \left(\int \rho_1(z, q') Q(q', q)\, dq' \right)^2 \\ &= \rho_1^2 Q - (\rho_1 Q)^2. \end{aligned} \tag{20}$$

We then need to average $Ve(z, q)$ over the distribution of (z_{a+1}, q_a), which is given by $P_{\bullet}M^a\mathrm{vec}(m_0)$. The environmental variation term is then

$$\text{environment trajectory luck} = \sum_{a=0}^{A-1} (\mathrm{vec}(V_e))^{\mathsf{T}} P_{\bullet}M^a m_0, \tag{21}$$

where we can calculate $\mathrm{vec}(V_e)$ as

$$\mathrm{vec}(V_e) = (\mathrm{vec}(\rho_1)^2)^{\mathsf{T}} Q - (\mathrm{vec}(\rho_1)^{\mathsf{T}} Q)^2. \tag{22}$$

Again, the dead state ω does not have to be included in the average because $V_e(\omega, \bullet) \equiv 0$.

Finally, there is fecundity luck. Conditional on the current state, we assume that success in different years is independent. The variance of success up to age A is therefore just the sum of the variances at each age: $\mathrm{Var}[R | \mathbf{x}, \mathbf{z}_{0:A}, \mathbf{q}_{0:A}] = \sum_{a=0}^{A} \sigma^2(\mathbf{z}_a, \mathbf{q}_a)$, where σ^2 is the variance in success in a given year. Thus,

$$\text{fecundity luck} = \sum_{a=0}^{A} \mathbb{E}_{\mathbf{z}_a, \mathbf{q}_a}(\sigma^2(\mathbf{z}_a, \mathbf{q}_a)). \tag{23}$$

Where These Calculations Break Down and What to Do About It

While the variance partition equations (1) and (3) hold so long as state and environment transitions occur in the sequence shown in figures 2 and 3, equations (2) and (4) and our calculation methods in the "Computing the Terms" section also depend on the additional assumptions that we stated above. Notably, for the three forms of trajectory luck as well as fecundity luck, we used the fact that we can break R up into two pieces, reproduction up through age a and reproduction at ages $a + 1$ and beyond, and that it is only the second piece that varies as a function of z_{a+1} (state trajectory) or q_{a+1}. This is true under our assumption that conditional on (z_a, q_a), immediate reproductive success is independent of all past and future events. But that assumption will not be true, for example, in a semelparous organism with a state-dependent probability of reproducing. If an individual is alive to possibly reproduce at age $a + 1$, then we know that it did not reproduce at age a or earlier, and thus reproduction up through age a (conditional on state and environment at age a) is not independent of the state at age $a + 1$. The same problem turns up whenever there are trade-offs between reproduction and survival or growth, so that an individual's state at age $a + 1$ is informative about whether it reproduced at age a. For example, if an individual is alive and reproducing at age $a + 1$, it is more likely to have had a higher survival rate, associated with not breeding, at age a.

In most cases, the situation can be rescued by enlarging the individual state variable z to include all information relevant to immediate reproductive success. In the case of a semelparous organism, the model could be implemented with the population censused immediately before reproduction but after it has been determined whether the individual reproduces that year. The state variable z is then augmented by a 0/1 variable distinguishing current year breeders from nonbreeders. In that setup, although reproduction at different ages is correlated, we still have the necessary property that conditional on individual (augmented) states and environments up to age a, reproduction at ages zero to a is independent of states at later ages.

The simplified decompositions (2) and (4) break down if the transition probabilities from the environment at time t to the environment at time $t + 1$ (or whatever event happens later in the time step) is not independent of the state at time t (or whatever gets updated first in the time step). Such correlations can be subtle. For example, we had hoped to further partition each component of luck into contributions from whether the individual ever breeds before death versus variation in the number of offspring given that they bred at least once, as in Snyder et al. (2021). However, that calculation involves the transition matrix/

kernel conditional on breeding before death, and with that conditioning the environment at time $t+1$ may not be independent of the state at time t. For example, consider a model where all sufficiently small individuals have never been large enough to breed and die if the next environment state is 1. Conditional on breeding before death, small enough size implies that the next environment state cannot be 1. Again, what breaks down is not the general variance partition (1) or (3) but the calculation formulas we provide to evaluate the terms. Analogous but more complicated formulas will apply, using the age- and state-dependent joint transition probabilities for individual state and environment conditional on breeding before death.

Case Studies

Tropical Trees in a Varying Light Environment

Our first case study uses size-structured IPMs of two tropical trees with time-varying light levels presented in Metcalf et al. (2009). The models were parameterized for lowland tropical rain forest trees at La Selva Biological Station in northwestern Costa Rica, based on the data provided by Clark and Clark (2006). We thank the authors of Metcalf et al. (2009) for providing unpublished R scripts and for additional information about their model development and implementation. The models and how we implemented them for our analyses are summarized in section S3 of the supplemental PDF.

We chose two canopy species for analysis, *Simarouba amara* and *Minquartia guianensis*, based on their contrasting responses to the light environment: “Small juvenile *Simarouba* exhibit the highest growth rate and the highest sensitivity to light, while small juvenile *Minquartia* and *Lecythis* have the lowest growth rates and relatively low sensitivity to light” (Metcalf et al. 2009, app. A, p. 1).

The models have a megamatrix structure (Pascarella and Horvitz 1998) in which individuals are cross classified by size z and light environment q (equivalently, they are size-quality models sensu Ellner et al. [2016, sec. 6.4.4] with (z, q) as the bivariate individual state). The smallest size at which individuals were measured is 1 mm, so there was already substantial mortality in the years when seedlings are still too small to be counted as recruits. Light levels 1, 2, and 3 represent low, medium, and high lateral light; level 4 represents some overhead light; level 5 is full overhead light; and level 6 indicates that the crown is fully exposed—either extending above the canopy or in a gap. Following Metcalf et al. (2009), an individual of size 300-mm dbh or larger is considered to be a canopy tree. We define lifetime success R to be the number of years in the canopy as a proxy for lifetime reproduction because we do not have a model for size-dependent fecundity.

The different light sensitivities of these species are reflected in the proportional importance of environment trajectory luck: environmental variation contributes only 4% to *Minquartia*’s overall luck but 21% to *Simarouba*’s.

Because tree growth is slow and steady, we expected that survival trajectory growth would be more important than growth trajectory luck, and that is true overall: survival trajectory luck contributes more than 75% of the variance in the number of years in the canopy for both species (fig. 4). However, for *Minquartia*, growth trajectory luck is the largest term at birth. This likely connects to survival in the end, however, because mortality is high for tiny trees, so young trees are most likely to reach the canopy if they leave the high mortality size window as quickly as possible.

The contributions of survival, growth, and environment trajectory luck peak at or near birth—the first step to a successful life is not dying young, and having some favorable years early on helps ensure that you do not die young. There are then secondary peaks or plateaus in the contributions of survival, growth, and environment trajectory luck, which occur at different ages.

The contribution of environment trajectory luck peaks just before the age at which most individuals reach the canopy. Environment trajectory luck at a given age is based on how much the next year’s environment will affect expected future success. Early in life, individuals are a long way from canopy height, so any one environment transition will not have much effect on the odds of eventual success. And once they have reached the canopy, trees usually stay there: shrinkage of large trees is rare, and when it happens, it is small. But just before an individual reaches canopy height, a good year can push them over the threshold or hold them back.

For *Minquartia*, a faint secondary peak in the contribution of growth trajectory luck occurs a little before trees typically reach the canopy, similar to the secondary peak in the contribution of environment trajectory luck. Getting a favorable year or some extra growth can boost a tree into the canopy. For *Simarouba*, there is an almost imperceptible secondary peak in the contribution of growth trajectory luck around the age when trees typically hit the canopy.

The contribution of survival trajectory luck peaks shortly after most individuals reach the canopy. Expected number of future years in the canopy is highest just after an individual reaches the canopy. Dying at an earlier age has less of an effect on expected years in the canopy, since young individuals are unlikely to reach the canopy and have a low expected value of success. Dying at a later age has less of an effect because the very largest trees have higher mortality than slightly smaller trees—as senescence looms, individuals have fewer expected years left.

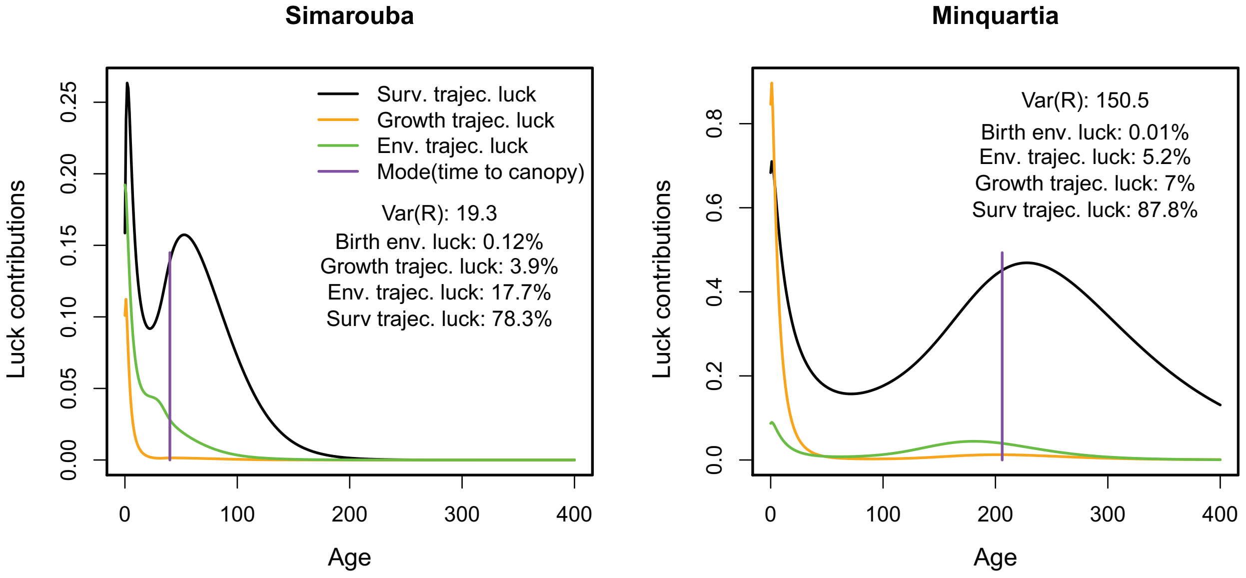

Figure 4: Contributions to variance in number of years spent in the canopy for tropical trees *Simarouba amara* and *Minquartia guianensis*. Note the different *y*-axis scales. The black lines are for survival trajectory luck, the orange lines are for growth trajectory luck, and the green lines are for environment trajectory luck. Fecundity luck is zero, since trees accumulate precisely one year in the canopy for each year they spend in the canopy. The purple lines show the age at which the largest proportion of individuals reach the canopy (the mode of the distribution). Because most trees die as seedlings, it is difficult to define a typical tree life span, but a *Simarouba* recruit has probability 0.013 of surviving to the modal age at entering the canopy, and a *Minquartia* individual has probability 0.009 of surviving to the modal age at entering the canopy. Figure generated by metcalfSurvGrowthPartitionSqrt.R, available at https://doi.org/10.5281/zenodo.6320885.

Artemisia ordosica

Artemisia ordosica is a dune-dwelling shrub found in Mongolia. We use the IPM presented in Li et al. (2011) with the parameters for a fixed dune with microbiotic crust. We have no environmental or trait data for this species, but we can investigate demographic luck. Section S1.2 of the supplemental PDF shows how to partition in the absence of environmental luck. Unlike our tree case studies, this shrub can shrink substantially, so we expect that growth trajectory luck may take on greater importance. We also expect growth trajectory luck to be important because in Snyder and Ellner (2016), we found that across all ages the probability of reaching 40 cm or taller (the sizes that produce most of the offspring) is most sensitive to changes in expected growth.

Figure 5 shows that our intuition was largely correct. While the contribution of survival trajectory luck is most important in the years immediately following birth, the contribution of growth trajectory luck soon overtakes it and remains dominant throughout the rest of life. In this example, we measure success by the number of years at 40 cm or taller, and so it is not surprising that growth trajectory luck peaks just before the age at which individuals most commonly reach these sizes: variation in growth at that age can boost an individual into the successful size range or hold them back.

Lomatium bradshawii

Lomatium bradshawii is an endangered herbaceous perennial found in a few grasslands and prairies in Oregon and Washington. It is fire adapted, and fire suppression is thought to be one reason for its decline. We used the demographic matrices for Rose Prairie site 1 from Kaye and Pyke (2003). There are five stages: seedlings, vegetative plants with one or two leaves, vegetative plants with three or more leaves, reproductive plant with one umbel, and reproductive plants with two or more umbels. Almost all seed production comes from the last stage. Our definition of success is lifetime seedling production.

We chose *Lomatium* because we wanted a case study with prominent environmental variation, and the data on *Lomatium* in Kaye and Pyke (2003) include results from a prairie-burning experiment (Kaye et al. 2001). Figure 6 shows that environment trajectory luck is in fact the largest contribution to variance in lifetime seedling production.

The times when the luck contributions peak are by now familiar. The contribution of environment trajectory luck peaks at the same age that most individuals hit the ≥2 umbel stage—that is, when most individuals start reproducing by seed. Fecundities vary substantially by year, so it is valuable to get a favorable year as soon as you become large enough to begin reproduction. However, the contribution of fecundity luck peaks the following year. Evidently the

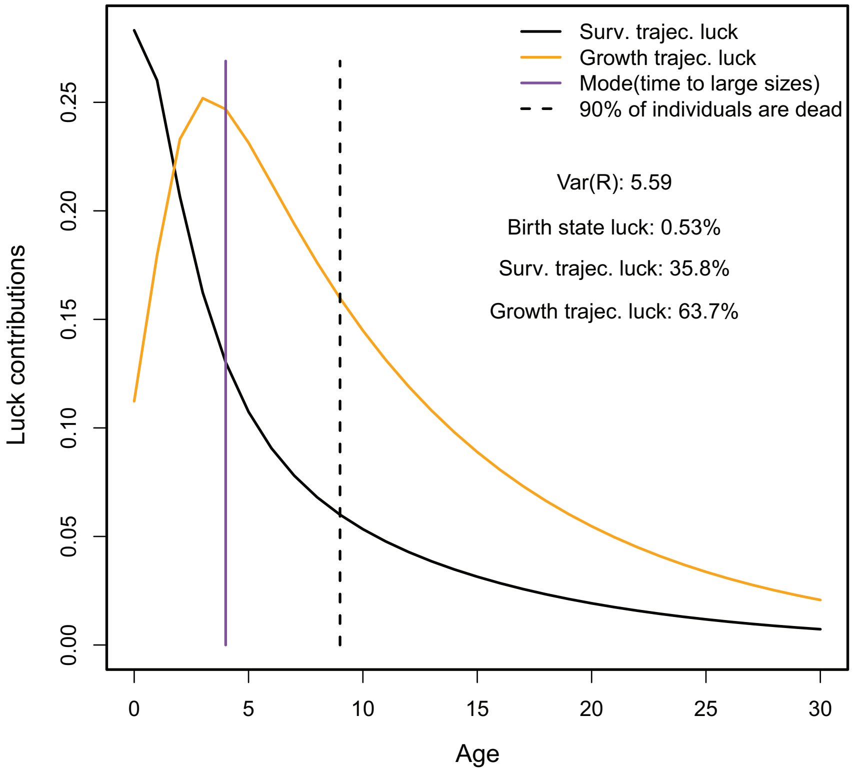

Figure 5: Contributions to variance in number of years spent at large sizes for *Artemisia ordosica*. The black line is for survival trajectory luck, and the orange line is for growth trajectory luck. There is no environmental variation in this model. Fecundity luck is zero, since individuals accumulate precisely one year at large sizes for each year they spend at large sizes. The purple line show the age at which the largest proportion of individuals reach the threshold size (the mode of the distribution), and the black dashed line shows the age by which 90% of individuals are dead. Figure generated by artemisiaSurvGrowthPartition.R, available at https://doi.org/10.5281/zenodo.6320885.

additional year of mortality is more than offset by the higher mean fecundity (and therefore higher variance in fecundity) because of expected growth during that year. The contribution of growth trajectory luck is also prominent and peaks the year before most individuals begin seed production (individuals need to transition into the final developmental class to get many seedlings), while the contribution of survival luck peaks at birth (do not die young).

Southern Fulmars

Southern fulmars (*Fulmarus glacioides*) are long-lived Antarctic seabirds. Fulmars forage near the ice edge, where productivity is high. In low-ice years, they must forage over longer distances to feed their chicks and breeding success is reduced, while high-ice years bring increased success. Jenouvrier et al. (forthcoming) presents a model in which individuals belong to one of three behavioral syndromes and are subject to time-varying sea ice levels. The model is structured by breeding status, with states consisting of prebreeders, successful breeders, failed breeders, and nonbreeders. The behavioral syndromes govern survival, breeding probability, and breeding success and are fixed traits (Jenouvrier et al. 2018*a*). For example, individuals exhibiting the group 2 behavioral syndrome tend to skip breeding more often than individuals in other groups and have the lowest juvenile survival, but they tend to have higher lifetime reproductive output than other groups under high-ice conditions because of their high adult survival. Jenouvrier et al. (2015) discretizes sea ice conditions (summarized by an index combining sea ice cover and the location of the sea ice edge) into three levels representing the bottom 10%, the middle 80%, and the top 10% and assumes that these levels occur at these frequencies. When discretized in this way, sea ice conditions are temporally uncorrelated (Jenouvrier et al. 2015).

The model we are using is one of very few that include both trait variation and effects of environmental variation. However, in order to fit that model with the available data it was necessary to omit age dependence in vital rates (S. Jenouvrier, personal communication), which is also known to be present (Jenouvrier et al. 2003). Thus, using this model may run the risk of overstating the importance

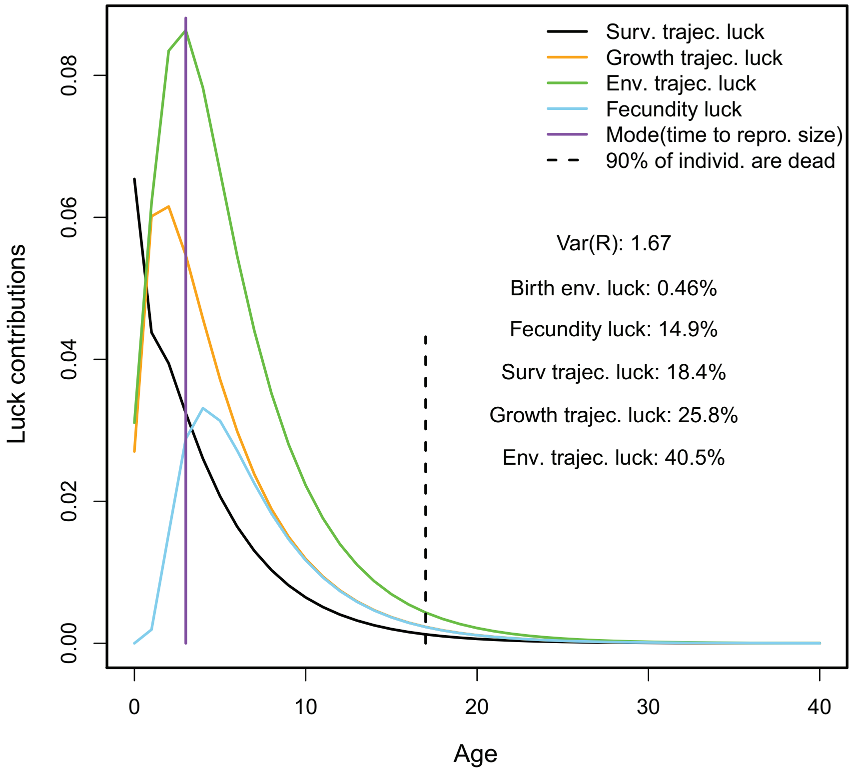

Figure 6: Contributions to variance in lifetime reproductive output for *Lomatium bradshawii*. The black line shows survival trajectory luck, the orange line shows growth trajectory luck, the green line shows environmental trajectory luck, and the light blue line shows fecundity luck. The purple line shows the age at which the largest proportion of individuals (the mode of the distribution) reach the two or more umbels class, which is responsible for almost all reproduction, and the black dashed line shows the age by which 90% of individuals are dead. Figure generated by lomatiumSurvGrowthPartition2.R, available at https://doi.org/10.5281/zenodo.6320885.

of environmental or trait variation. Nevertheless, we find that the contribution of survival trajectory luck dominates in groups 1 and 3, and the contributions of survival, growth, and environment trajectory luck all peak at roughly the same time (fig. 7). The timing of these peaks arises from a balance: at older ages more individuals have moved beyond the prebreeder stage, where demographic and environmental transitions matter more, while at younger ages individuals are more likely to still be alive. Group 1 as a whole loses individuals to death more slowly than other groups, and so the balance tips toward later ages: the luck contributions peak at age 10, when the population of successful breeders (stage 2) is at its highest. For behavioral group 2, however, early luck is driven by the contribution of growth trajectory luck—transitions among breeding statuses. This is because individuals in group 2 have lower prebreeder survival than the other groups, so it is important to transition quickly to the successful breeder group. The contribution of survival trajectory luck never reaches the heights that it does for the other groups because by the time it peaks, many group 2 individuals have died (e.g., a newborn group 2 individual has a 48% chance of surviving to age 10, compared with a 77% chance for group 1 and 61% for group 2.)

The contribution of fixed trait variation comes in when we compare the performance of individuals in the three behavior groups, shown in the lower right panel of figure 7. Age partitioning of the contribution of traits can be done by a simple extension of the methods developed in Snyder et al. (2021); we present a summary in section S2 of the supplemental PDF.

We explored the effect of temporal autocorrelation in the environment by changing the environment transition matrix Q to $Q_{\text{new}} = \phi I + (1 - \phi)Q$, where I is the identity matrix. That is, the environment remains in its current state with probability ϕ and otherwise changes according to the actual transition probabilities (which also include the possibility of staying in the same environment). This keeps the long-term frequencies of different environment states the same (because Q_{new} has the same eigenvectors as Q) but adds positive temporal autocorrelation. Because the transition matrix Q has zero autocorrelation, it can be shown that the correlation between the current environmental state and next year's state equals ϕ. We found that

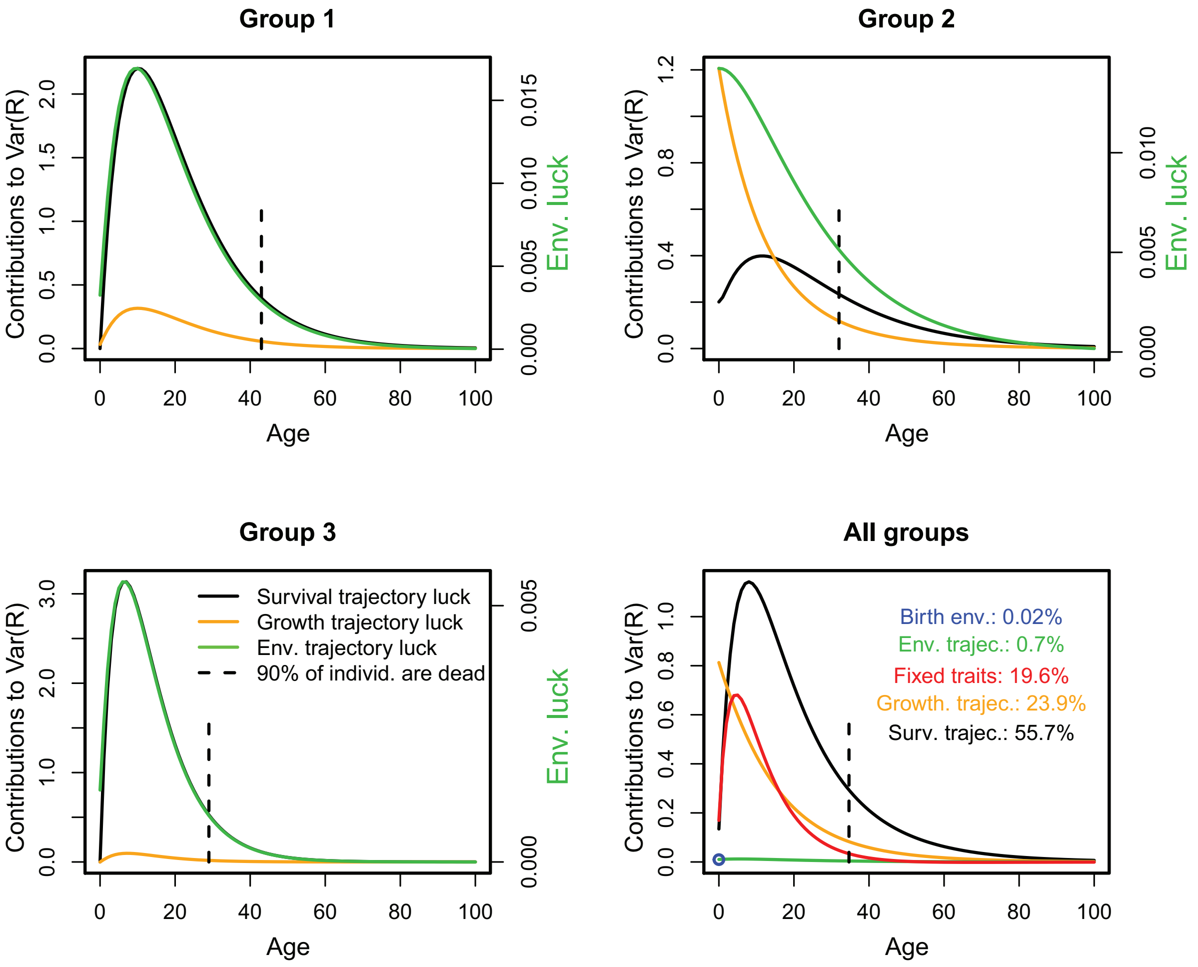

Figure 7: Contributions to variance in lifetime reproductive output for southern fulmars (*Fulmarus glacioides*). The black lines show survival trajectory luck, the orange lines show growth trajectory luck, and the green lines show environment trajectory luck. Note the different *y*-axes as well as the dual axes: environment trajectory luck is much smaller than survival trajectory luck. The black vertical dashed lines show the mean lifetime. The bottom right panel shows weighted averages across groups as well as the contribution of trait variation. Figure generated by fulmarSurvGrowthPluckPartition.R, available at https://doi.org/10.5281/zenodo.6320885.

as temporal autocorrelation increases, environment trajectory luck and birth environment both matter more. For example, for the original model ($\phi = 0$), the contribution of birth environment luck is 0.01 and the contribution of environment trajectory luck is 0.376, while when $\phi = 0.5$, their contributions are 0.034 and 0.931, respectively. Positive autocorrelation increases the importance of environmental luck because whatever environment state you experience in the next time step, you are more likely to be stuck with it for a while.

Discussion

At the beginning of this article, we asked how much success is driven by individual quality versus external factors versus random chance. We have shown how to partition the variance of some measure of lifetime success into a contribution from fixed trait variation plus age-specific contributions from different kinds of demographic and environmental luck. We assume that each individual experiences their own Markovian sequence of environment states, independent of what other individuals are experiencing. If the environment varies over a fine spatial scale as well as temporally, so that individuals do experience independent environments, then this individual-level variance is the variance across individuals within the population. Otherwise, we are partitioning into different components the variance of an individual's success over an imagined ensemble of replicate lifetimes.

Our empirical examples in earlier work indicated that adult life span is an important driver of luck (Snyder and Ellner 2018), which led us to suspect initially that the contribution of survival trajectory luck would typically predominate. The contribution of survival trajectory luck is indeed dominant for organisms that exhibit slow and steady growth through sizes or stages, such as trees. However, the contribution of growth trajectory luck can dominate at most ages for organisms with more variable growth, such as our shrub case study. External factors—environment at birth and the sequence of subsequent environment states—can predominate for organisms that rely on disturbance or other infrequent environment conditions, such as in our fire-adapted perennial case study.

Variation in individual quality continues to play a lesser role in empirical examples. In theory, individual quality variation can be the dominant factor. But as we argued in Snyder and Ellner (2018), whenever the distribution of success (by whatever measure) is skewed so that only a "lucky few" are highly successful, natural selection will quickly weed out genotypes that have no chance of becoming one of the lucky few, so the link between traits and success is blurred. More generally, when theoretical models are constrained by empirical estimates of fitness variation in the wild, the impact of quality variation never exceeds that of luck (Snyder and Ellner 2018). Hypothetical populations on the computer can have any trait distribution and any trait impacts, but if the traits are heritable things will be very different after a few generations of natural selection. Large impacts of persistent trait variation are most likely when the variation is not heritable, such as persistent variation in individual performance among plants due to attributes of the site where they are rooted.

Luck contributions tend to peak soon after birth and again around the time when most individuals are first becoming successful. When success comes a long time after birth, as it does for trees, this produces two sets of luck peaks. The contributions of survival, growth, and environment trajectory luck often peak at different times, however, offering insight into why luck is important at that age. For example, a favorable environment can push a tree into the canopy, while high survival just after they get there allows them to take advantage of it. Environment trajectory luck becomes more important as the environment becomes positively autocorrelated. The longer this year's environment is likely to persist, the more important it is whether those conditions are favorable or unfavorable.

We used multiple definitions of individual success in this article—lifetime reproductive output, number of years at sizes with high reproductive success—and can imagine others, including binary outcomes such as reaching a critical size or life stage (e.g., canopy height) or not. One benefit of our approach is that the same theory and formulas apply to all of these, so that different facets of the life history and different components (or definitions) of fitness can all be examined. Our approach can be used whenever (1) one can calculate the mean and variance of the lifetime success measure as a function of starting state, (2) dynamics are Markovian (the state at time t depends only on the state at time $t-1$), and (3) the transition probabilities from the environment at time t to the environment at time $t+1$ (or whatever event happens later in the time step) is independent of the state at time t (or whatever gets updated first in the time step). So what we have been calling "environment" can in principle be any variable that affects individual performance or state dynamics without being affected by them.

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Christophe Barbraud and Stéphanie Jenouvrier graciously shared the environment- and trait-dependent fulmars model projection matrices with us. Nick Kortessis made us realize that this article is about partitioning outcome variation among individual quality, external factors, and random chance. Lee Smith nudged us to consider a case study in a disturbance-dominated environment. We thank Stéphanie Jenouvrier, Karen Abbott, and members of the Abbott lab for helpful presubmission comments and our editors (Erol Akçay, Marc Mangel) and reviewers (Edgar J. González, Jody Reimer) for many suggestions that further improved the manuscript. This research was supported by National Science Foundation grants DEB-1933497 (S.P.E.) and DEB-1933612 (R.E.S.). The Institute Paul Emile Victor (program IPEV 109) and Terres Australes et Antarctiques Françaises provided logistical and financial support for fulmar data collection by Barbraud and Jenouvrier.

Statement of Authorship

Both authors were equally involved in all stages of research and manuscript preparation.

Data and Code Availability

Code for the case study partitioning figures is available on Zenodo (https://doi.org/10.5281/zenodo.6320885; Snyder and Ellner 2022).

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Snared in an evil time: how age-dependent environmental and demographic variability contribute to variance in lifetime outcomes,

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S1 Calculating state trajectory luck and partitioning in the absence of environmental variation

S1.1 Computing state trajectory luck

In eqn. (2) state is updated first, then environment. We therefore need a function giving expected success at ages $a+1$ and above, conditional on z_{a+1} (the updated state) and q_a (the current environment). We will call this $\rho_1^*(z,y)$, and it can be computed as

$$\rho_1^*(z,y) := \mathbb{E}[\rho_1(z,q_{a+1})|q_a = y] = \int \rho_1(z,y')Q(y',y)\,dy'. \tag{S1}$$

For computing: if ρ_1 is stored as a matrix with (i,j) entry $\rho_1(z_i,q_j)$, then (S1) is a single matrix multiplication $\rho_1^* = \rho_1 Q$.

Returning to (1), the variance in the state trajectory luck is the variance (across different possible next states z_{a+1}) of expected reproduction at ages $a+1$ and beyond, conditional on state z_{a+1} and environment q_a. That is, it is the variance of $\rho_1^*(z_{a+1},q_a)$ across the distribution of z_{a+1} conditional on z_a, q_a, and x. That variance, as a function of z_a, q_a, is given by

$$V_s(z,q) = \int \rho_1^*(z',q)^2 P_q(z',z)\,dz' - \left(\int \rho_1^*(z',q)P_q(z',z)\,dz'\right)^2. \tag{S2}$$

Note that the integrals on the right-hand side do not need to include ω, because $\rho_1^*(\omega,q) \equiv 0$. Because the kernel on the right-hand side depends on q, values of V_s for each q need to be computed separately. A direct approach is to do

$$V_s(\bullet,q) = \text{vec}(\rho_1^*(\bullet,q)^2)^\top P_q - (\text{vec}(\rho_1^*(\bullet,q))^\top P_q)^2 \tag{S3}$$

for each q and fill in V_s by a loop over q values.

Alternatively, let $P_\bullet$ denote the megamatrix-size block-diagonal matrix in which the blocks are the state-transition or iteration matrices P_q for environment states $q_1, q_2, \cdots$. $P_\bullet$ can be built easily as a sparse matrix in R if the set of P_q matrices are stored as a list, using the function `bdiag_m` that is on the help page for `bdiag` in the **Matrix** library. Then

$$\mathrm{vec}(V_s) = (\mathrm{vec}(\rho_1^*)^2)^\mathsf{T} P_\bullet - (\mathrm{vec}(\rho_1^*)^\mathsf{T} P_\bullet)^2. \tag{S4}$$

We then need to average over the distribution of (z_a, q_a), which is given by $M^a\,\mathrm{vec}(m_0)$. The decomposition of state trajectory luck is then

$$\text{State trajectory luck} = \sum_{a=0}^{A-1} (\mathrm{vec}(V_s))^\mathsf{T} M^a\,\mathrm{vec}(m_0). \tag{S5}$$

S1.2 Partitioning in the absence of environmental variation

When there is no environmental variation, survival and growth trajectory luck become

$$\begin{array}{ll} \sum_{a=0}^{A-1} \mathbb{E}_{\mathbf{x},\mathbf{z}_a}\left\{Var_{\mathbf{z}'_{a+1}|\mathbf{x},\mathbf{z}_a}[\mathbb{E}(R|\mathbf{x},\mathbf{z}'_{a+1})]\right\} & \text{Survival trajectory luck} \\ +\ \sum_{a=0}^{A-1} \mathbb{E}_{\mathbf{x},\mathbf{z}'_{a+1}}\left\{Var_{\mathbf{z}_{a+1}|\mathbf{x},\mathbf{z}'_{a+1}}[\mathbb{E}(R|\mathbf{x},\mathbf{z}_{a+1})]\right\}. & \text{Growth trajectory luck} \end{array} \tag{S6}$$

We define

$$\rho_1''(z') := \mathbb{E}(\rho_1(z_{a+1})|z'_{a+1} = z') = \int \rho_1(z) G_q(z,z')\,dz, \tag{S7}$$

and in place of eq. (13), we have

$$V_s(z) = \int (\rho_1''(z'))^2 S_q(z',z)\,dz' - \left(\int \rho_1''(z')^2 S_q(z',z)\,dz'\right)^2. \tag{S8}$$

We can then use eq. (15) to calculate survival trajectory luck. In place of eq. (17), we have

$$V_g(z') = \int (\rho_1(z))^2 G_q(z,z')\,dz - \left(\int \rho_1(z) G_q(z,z')\,dz\right)^2, \tag{S9}$$

and we then use eq. (19) to calculate growth trajectory luck.

S2 Age-partitioning the contribution of fixed trait variation in the presence of environmental variation

The contribution of trait variation is given by $Var_x[\mathbb{E}(R|\mathbf{x})]$. To age-partition this term, as in Snyder et al. (2021) we first evaluate it under the assumption that trait variation disappears after age a, and then calculate the term as the sum of the marginal changes in value as the threshold age is sequentially increased from 1 to ∞.

More precisely, let $\vec{x} = (x_0, x_1, x_2, \cdots)$ be a vector of the individual's trait at all ages, and let x^* denote a trait value such that individuals with trait x^* have trait-averaged state/environment transition matrix/kernel, $\overline{M} = \int M_x p_0(x)\, dx$ and the trait-averaged fecundity matrix/kernel $\overline{F} = \int F_x p_0(x)\, dx$, where $p_0(x)$ is the trait distribution. Define

$$\begin{aligned} v_{-1} &= Var_x\, \mathbb{E}(R|\vec{x} = (x^*, x^*, x^*, \cdots)) = 0 \\ v_0 &= Var_x\, \mathbb{E}(R|\vec{x} = (x, x^*, x^*, \cdots)) \\ v_1 &= Var_x\, \mathbb{E}(R|\vec{x} = (x, x, x^*, \cdots)). \end{aligned} \tag{S10}$$

We then have

$$Var_x[\mathbb{E}(R)] = (v_0 - v_{-1}) + (v_1 - v_0) + (v_2 - v_1) + \cdots \tag{S11}$$

and the marginal increase $(v_a - v_{a-1})$ is the age-a contribution to the total contribution of fixed trait variation to variation in R.

The age-specific contributions can be evaluated by just substituting megamatrix state/environment and fecundity kernels for their constant-environment counterparts in the formulas derived by Snyder et al. (2021, p. E121), giving

$$v_a = Var_x\left(\rho_{0,a}(x)\right), \tag{S12}$$

for

$$\rho_{0,a}(x) = \mathbf{A}_x + \mathbf{b}_x^{\mathsf{T}} M_x^a m_{0,x}, \tag{S13}$$

$$\text{where } \mathbf{A}_x = \mathbf{e}^{\mathsf{T}} F_x N_x m_{0,x} \text{ and } \mathbf{b}_x^{\mathsf{T}} = \mathbf{e}^{\mathsf{T}} (\overline{F}\,\overline{N} - F_x N_x) M. \tag{S14}$$

S3 Models for tropical trees in a varying light environment

Our analyses, like those of Metcalf et al. (2009), concern only growth and longevity rather than actual reproductive output, so only survival and growth need to be modeled as functions of individual size and light environment. The size measure is continuous — the natural log of tree diameter (mm dbh) — and light environment is discrete, with six categories (Metcalf et al. 2009, p. 2678): values 1, 2, and 3 indicate low, medium, and high lateral light only, 4 indicates some overhead light, 5 indicates full overhead light, and 6 indicates that the crown was completely exposed (either emergent from the canopy or in a gap).

In order to visualize and inspect the models relative to the data, we downloaded the Clark and Clark (2006) data set (the online file `LS_trees_1983_2000.txt` linked to that paper). Using code provided by the authors of Metcalf et al. (2009), we extracted from it a data frame with the following variables:

- `d.t0, logd.t0`: Size and log-transformed size at an annual census.
- `d.t1, logd.t1`: Size and log-transformed size at the subsequent annual census.
- `surv`: did the tree with initial size `d.t0` survive to the subsequent census?
- `Q.t0`: light environment category of each tree at an annual census corresponding to `d.t0`.
- `light`: factor variable indicating the higher light environment categories (4,5,6).

Because tree mortality is relatively rare, Metcalf et al. (2009) fitted a relatively simple survival model for each species, with only two light environment categories and a single slope:

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```
sfit=glm(surv∼ logd.t0+light,family="binomial")
```

Here `logd.t0` is the log of tree diameter at an annual census, `surv` indicates whether or not the tree survived to the next census, and `light` is a factor variable with value `TRUE` indicating light environments 4,5,6 and value `FALSE` indicating light environments 1,2,3. The model assumes a constant slope of logit survival versus size, and an intercept that differs between the lower three and the higher three light environments.

To account for size-dependent growth variance, Metcalf et al. (2009) fitted the growth model by generalized least squares using the `gls` function in the **nlme** package:

```
gfit.SA=gls(logd.t1∼ logd.t0*factor(Q.t0),weights=varExp(form= ∼ fitted(.)))
```

Because mortality is rare, there are many observations of growth from one year to the next (6637 for *Simarouba*, 2895 for *Minquartia*), so this model included a slope and intercept that both depend on the 6-level classification of light environment.

Figure S1 shows the fitted survival and growth models. Feeling obliged to follow our own published advice (Ellner et al., 2016), we carried out some graphical model diagnostics. We did find evidence of some small imperfections, but as these involved a very small fraction of the data, we saw no reason to try fitting more complicated models. Details follow, if you're interested.

The fitted survival functions seem to capture the trends in the binned survival estimates, except for very small trees in higher light conditions. There, the binned survival estimates remain high while the fitted models have a decline in survival at the smallest sizes. However, because the smallest trees rarely occur in higher light environments (i.e., the red points for initial log size < 3 are massively out-numbered by the gray points), this discrepancy affects an inconsequential number of individuals. We therefore left the model as-is rather than adding parameters to make it "wag its tail" in the direction of a few stray data point.

The growth models are similarly plagued by a few outlier observations, which lie far outside the fitted growth model's prediction. But again, these are a few dozen points out of thousands, so we made no attempt to complicate the model to accommodate them. In a study of this size

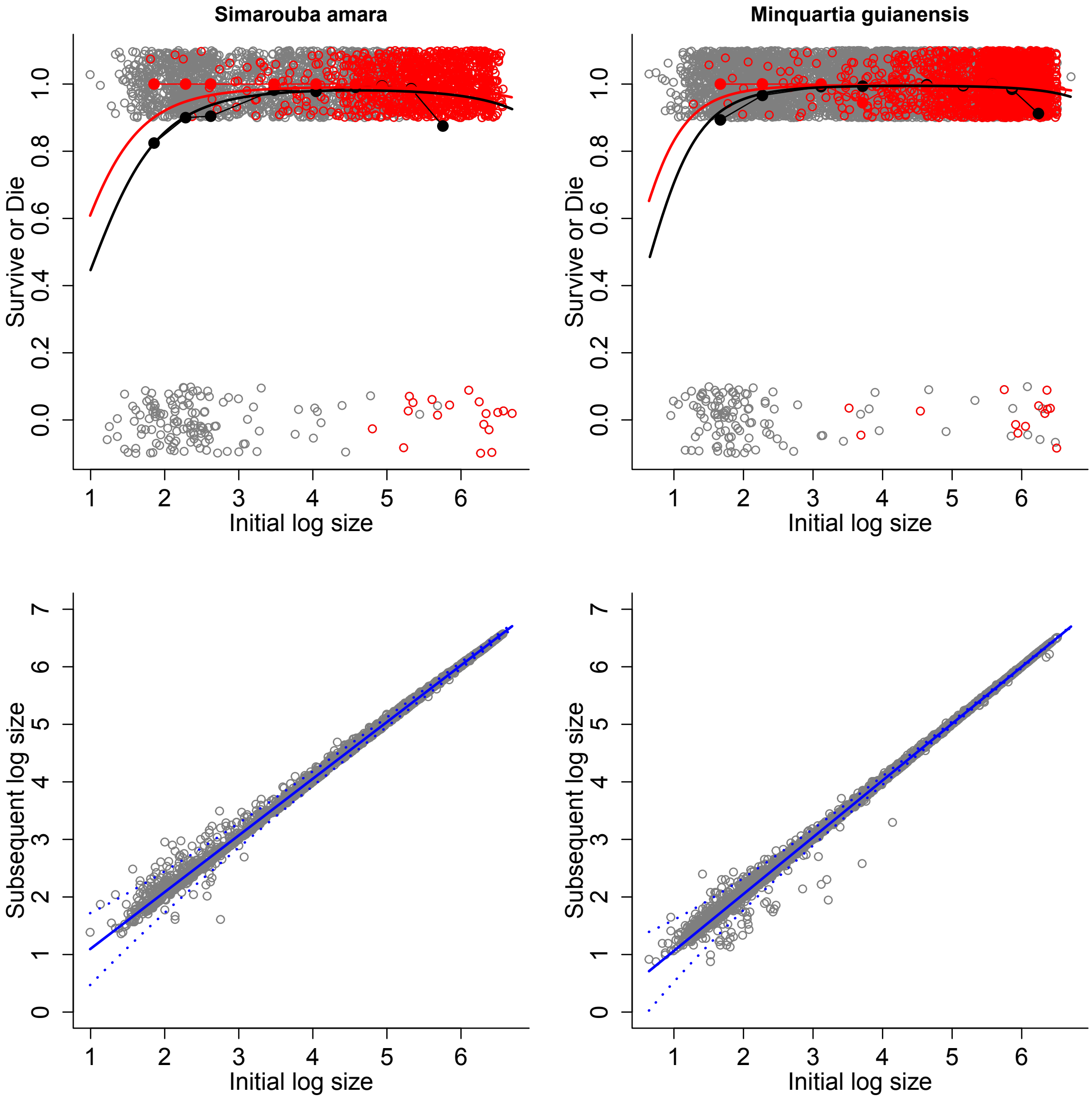

Figure S1: Survival (top) and growth (bottom) models for our focal species. Survival: Values 0 and 1 corresponding to death or survival have been jittered. Colors gray and red indicate lower (categories 1,2,3) versus high (categories 4,5,6) light conditions. The colored curves are the fitted logistic regression models. The solid circles connected by lines are average survival in size categories defined by quantiles of initial log size, plotted against the median log size of individuals in that quantile. Growth: solid blue line is the predicted mean subsequent size, combining data from all light categories. The dotted blue curves are the predicted mean ±2 times the fitted size-dependent standard deviation of growth increments.

and duration, it seems quite possible to us that shrinkage of a medium-size tree by 50% or more is perhaps best explained as somebody measuring the wrong tree.

At the smallest sizes, the observed growth increments appear to lie slightly above the fitted linear model. Fitting growth with a spline instead of a linear model, we did find a slight curvature in the fitted mean growth at the smallest sizes. However, this apparent deviation in the mean is small relative to the variability in growth, and is driven by small number of data points, so we again chose to retain the linear model.

The validity of the exponential model for size-dependent variance (apart from the outliers) is hard to assess visually in these plots. We therefore made plots of scaled residuals (i.e., residuals divided by the fitted standard deviation) against fitted values for both models. If the exponential model is correct, the scaled residuals should be homoscedastic, and the plots (not shown) did not suggest any heteroscedasticity. As a more quantitative check, we re-fitted the variance models nonparametrically, using the `gam` function in the **mgcv** package (Wood, 2017) with `family=gaulss`. In both cases, the log of the fitted standard deviation had a close to linear decline with initial log size, which corresponds to the exponential variance model used in the `gls` fit of the growth model.

The strong size-dependence in growth variance on log-scale makes it difficult to work with the model, because a very large number of mesh points is needed to resolve the growth distribution at the largest sizes. (Metcalf et al. (2009) only modeled trees' lives prior to reaching the canopy, and therefore did not encounter this problem.) We therefore implemented the models numerically using the square root of dbh, rather than log dbh, as the size measure. The underlying demographic functions are all retained, but the growth variance expressed on square root scale is only weakly dependent on size, and 500 mesh points was sufficient to get accurate numerical results using integrated bin-to-bin calculations of the projection matrices. Our check for numerical accuracy was to compare the variance of LRO computed directly (using sec. 3.2.2 of Ellner et al. (2016)) with the sum of all terms in our partition, because these are two entirely distinct and separate calculations of the same quantity. The difference between them decreased with increasing number of mesh points, and with 500 mesh points the relative error was a fraction of a percent for both species.

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