Pluck or luck: does trait variation or chance drive variation in lifetime reproductive success?

Robin E. Snyder[1,*,†]
Stephen P. Ellner[2]

1. Case Western Reserve University, Cleveland, Ohio 44106;
2. Cornell University, Ithaca, New York 14853.
∗ Corresponding author; e-mail: res29@case.edu
† The authors wish to be identified to the reviewers.

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Abstract

While there has been extensive interest in how intraspecific trait variation affects ecological processes, outcomes are highly variable even when individuals are identical: some are lucky while others are not. Trait variation is therefore only important if it adds substantially to the variability produced by luck. We ask when trait variation has a substantial effect on variability in lifetime reproductive success (LRS), using two approaches: 1) we partition the variation in LRS into contributions from luck and trait variation; 2) we ask what can be inferred about an individual's traits, and with what certainty, given their observed LRS. In theoretical stage- and size-structured models, and two empirical case studies, we find that luck usually dominates the variance of LRS. Even when individuals differ substantially in ways that affect expected LRS, unless the effects of luck are substantially reduced (e.g. low variability in reproductive lifespan or in annual fecundity), most variance in lifetime outcomes is due to luck, implying that departures from "null" models omitting trait variation will be hard to detect. Luck also obscures the relationship between realized LRS and individual traits. While trait variation may influence the fate of populations, luck often governs the lives of individuals.

Introduction

The last two decades have seen a surge in interest among ecologists in intraspecific variation and its ecological consequences (e.g. Bolnick et al., 2011), including discussions about how trait differences between individuals might promote or suppress species coexistence (Barabás and D'Andrea, 2016; Bolnick et al., 2003; Clark, 2010; Hart et al., 2016; Lichstein et al., 2007), stabilize population dynamics (Agashe, 2009; Imura et al., 2003), reduce demographic stochasticity (Fox et al., 2006; Kendall and Fox, 2002), increase population growth rate (de Valpine, 2009; de Valpine et al., 2014; Kendall et al., 2011), and promote productivity (Hughes et al., 2008). Common to all of these discussions is the understanding that it is not trait variation per se that matters, but its effect on individuals, populations, and communities. Demographic studies that collect data on marked individuals over their lifetimes often find evidence for persistent individual differences in demographic rates such as expected clutch size and survival (e.g., Cam et al., 2012, 2016; Chambert et al., 2013; Hamel et al., 2009; Plard et al., 2012, 2015a,b,c). But recent theory has revealed that even if all individuals are identical (e.g., if all have the same age-specific expected fecundity and risk of death), there is high variability in outcomes: some individuals are lucky while others are not (Caswell, 2009, 2011; Snyder and Ellner, 2016; Steiner et al., 2010; Tuljapurkar et al., 2009; van Daalen and Caswell, 2017)[1]. Persistent between-individual variation ("trait variation") is therefore only important if it adds substantially to the variability in individual success produced by simple luck. Some empirical case studies suggest that in fact the effects of luck can greatly exceed those of trait variation (Bonnet and Postma, 2016; Orzack et al., 2011; Steiner et al., 2010; Tuljapurkar et al., 2009). Is this inevitably the case?

In this paper we begin to address that question by asking when persistent trait variation has a substantial effect on the among-individual variability in lifetime reproductive success (LRS). While we plan to expand our investigation to other demographic quantities of interest, such as population extinction risk, we begin with LRS for two reasons. First, LRS is a measure of dynamics over a single generation, so we can investigate the effects of a given level of trait variation without having to model inheritance and predict how trait variation changes over multiple generations (which can be tricky for traits affecting growth in a size-structured population (see Chevin, 2015; Janeiro et al., 2017; Plard et al., 2012; Vindenes and Langangen, 2015).

Second, some have proposed using the variance of LRS to test for the presence of significant trait variation: if the variance in LRS can be explained by a model without trait variation, then trait variation can be neglected (Orzack et al., 2011; Steiner and Tuljapurkar, 2012; Steiner et al., 2010; Tuljapurkar et al., 2009). For example, from Steiner et al. (2010): "We demonstrate that the estimated multi-stage model [without individual differences] can serve as a 'null' model, that is, one that can explain observed life history patterns without appeal to latent individual traits fixed at birth. Fixed differences should increase the variance in lifetime reproductive success (LRS) and survival compared to the null model; we do not observe such an increase. Our results show that the variation among individuals in their life histories can be explained solely by dynamic heterogeneity[2]." Such findings go against our intuition that large differences in individual outcomes should have a biological cause – some detectable difference between the individuals.

[1] The chance variation in outcomes for a single individual that we call "luck" has also been termed "individual stochasticity" (Caswell, 2009) and "dynamic heterogeneity" (Tuljapurkar et al., 2009).

[2] Steiner et al. use "dynamic heterogeneity" to refer to luck, environmental variation, and any other source of variation not related to persistent individual differences.

When, and how much, does trait variation matter for variation among individuals in LRS? We address this question in two ways. First we ask when we would expect the variance in LRS to be substantially affected by trait variation. Then we ask if individuals with high LRS are generally those with the best trait values, or if their success is largely a matter of luck: if an individual had many offspring during its life, can we infer that it was a high-quality individual? We investigate these questions first in analytically tractable simple models for a two-stage life cycle, either iteroparous or semelparous. Our tragically finite life spans prevent us from considering the full spectrum of more complicated life cycles, but as a partial check on the robustness of our conclusions from the two-stage models, we also consider the opposite extreme, continuous variation in "stage". For this we use a size-structured model patterned after typical integral projection models (IPM) for populations in constant environments.

Finally, we use the insights from these analyses to interpret the results of two empirical case studies, where there is substantial variation in traits affecting demographic rates. The first case study is the black-legged kittiwake (*Rissa tridactyla*) in which adult survival and breeding probability vary between individuals, based on demographic studies by E. Cam and collaborators (e.g., Cam et al., 2002, 2012) and the age- and stage-structured model of Steiner et al. (2010). We chose this case study because kittiwakes have been central to the ongoing controversy about how much individual "quality" variation contributes to variation in LRS, and as a result we can take advantage of previous modeling efforts based on extensive long-term field studies. The second case study considers the shrub *Artemisia tripartita* and the perennial grass *Pseudoroegneria spicata* in Idaho (USA) sagebrush steppe (Adler et al., 2010; Chu and Adler, 2015), using extensions of the integral projection models previously developed for these species (Adler et al., 2010; Chu and Adler, 2015). This case study was one of the original motivations for this paper and its antecedent (Snyder and Ellner, 2016). The focal trait in these species is the strength of competition from neighboring plants in the initial year of life. This "trait" is an attribute of the individual's location, rather than the individual, but the questions and methods are the same. Of the many seeds that an adult plant typically produces over its lifetime, only a tiny fraction survive to become an adult with high LRS. We wanted to know, which seedlings are the lucky ones? Is it pure luck, or is it possible to pick the winners in advance? New seedlings that are too close to a large established conspecific plant have very high mortality (as we will show below), so we hypothesized that variation in the competition neighborhood of new seedlings would explain a lot of the variation in lifetime reproductive success.

We were wrong. In our general stage- and size-structured models, and in both empirical case studies, we find that luck, not trait variation, generally contributes most of the variability in LRS unless other sources of variability are drastically restricted. For the plants in particular, the importance of trait variation relative to luck turned out to be much, much smaller than intuitive expectations. The high importance of luck implies that individuals' trait values generally cannot be inferred from their observed LRS. Given this disconnect between traits and LRS, we conclude with a brief discussion of what these findings imply for selection and trait evolution. Not surprisingly, one impact of trait-independent variability in LRS is to increase random drift (potentially by quite a bit) but we also find that it increases the expected rate of trait change due to selection.

We show in Supplemental Information section *Selection* that the luck-based correction term for selection decreases as constant/population size, and we expect all population-level quantities to have a similar scaling, since they involve averages over populations. Nonetheless, the scaling

with population size may be slow in some situations, so that effects of luck will only average out in very large populations. To the degree that luck has a substantial influence on population-level quantities our results raise questions for trait-based ecology and microevolution. When population-level outcomes like total number of offspring, or total number of prey captured, are largely due to luck, a focus on within-species trait variation may not be very fruitful for explaining ecological patterns.

Measures for the Importance of Trait Variation

Partitioning variation in LRS

We partition variation in lifetime reproductive success, R, into contributions from luck and contributions from between-individual variation in a trait x, using the standard variance decomposition formula from probability theory,

$$Var(R) = \underbrace{\mathbb{E}_x(Var(R|x))}_{\text{luck}} + \underbrace{Var_x(\mathbb{E}(R|x))}_{\text{trait variation}}. \tag{1}$$

The second term in eq. (1) is variance in LRS due to the "main effect" of trait value; the first term is residual variation ("luck") that is not explained by trait differences. The ratio between the trait variation term and the total variation, $Var_x(\mathbb{E}(R|x))/\,Var(R)$, is analogous to heritability in quantitative genetics: it is the fraction of total variation accounted for by the main effect of the trait (in the ANOVA sense). We use this ratio in our analyses to summarize the relative importance of trait variation versus luck.

Equation (1) is applied in different ways for our various models. For the general two-stage models, the terms in (1) can be calculated or approximated analytically, as we explain in Appendix A. For the prototype size-structured IPM, we use methods in Ellner et al. (2016, Ch. 3) to calculate $\mathbb{E}(R)$ and $Var(R)$ as a function of individual trait and initial size; from those, both terms on the right-hand side of (1) can be calculated (details are in Appendix B). Calculations for the kittiwake and perennial plant models are detailed in the sections for those models. For the perennial plants, we also decompose the luck term into contributions from different sources of variability (e.g., first-year survival and growth versus later events, and (as in van Daalen and Caswell, 2017) variation in lifespan versus variation in age-dependent fecundity).

Inferring traits from realized LRS

We can also explore the role of luck by asking how much we can infer about an individual's traits from their LRS and how precisely: are all of the individuals in the upper tail of the LRS distribution necessarily individuals with above-average traits? Mathematically, we are interested in studying $\Pr(x|R)$. Using Bayes' theorem, we can express this as

$$\Pr(x|R) = \frac{\Pr(R|x)\Pr(x)}{\Pr(R)} = \frac{\Pr(R|x)\Pr(x)}{\int \Pr(R|x)\Pr(x)dx}, \tag{2}$$

where $\Pr(x)$ is the trait distribution, a component of each model.

Two-stage Models

Models

To explore general properties, we analyze some simple models of an iteroparous and a semelparous life history with two discrete life stages, Juvenile and Adult. Notation is summarized in Table 1. For both models, a juvenile has probability s_J of surviving to adulthood (reproductive maturity). Given survival to maturity, time to maturity is immaterial for lifetime reproductive success (because of this, the two-stage model with $s_J = 1$ is mathematically equivalent to a one-stage model with regard to the distribution of LRS, so the two-stage model can also represent an annual species or a perennial without an immature stage). Lifespan as an adult is a random variable D, with mean L (which is ≥ 1 because survival to adulthood implies that an individual attempts breeding at least once), and variance $Var(D)$. We assume that stage matters but not age or prior reproductive success, hence the distribution of annual reproductive success ("offspring number") is the same for each year of life as an adult, and independent of past reproduction. Expected annual offspring number is denoted F, and C_i denotes the random realized offspring number in the i^{th} year of adulthood.

Iteroparous model: Each year of life as an adult, an individual produces a clutch with expected size F. Lifespan as an adult may be constant or random.

Semelparous model: Each year of adulthood, individuals die with probability d and reproduce with probability b. Reproduction is fatal; thus, conditional on reaching adulthood, life ends in reproduction with probability $b/(d+b)$ and ends in death without reproduction with probability $d/(d+b)$.

The parameters s_J, F, L, d, and b will be considered as traits that might vary among individuals in the population. These are not traits in the usual sense (wing length, immunocompetence, etc.). But it is the values and variation of these demographic parameters that determine the impact of among-individual variation on LRS, so for our purposes these are the "traits" that really matter.

When there is between-individual trait variation, we will be concerned with two distinct variances for life-history attributes such as LRS: the population variance, and the variance given the trait value. For example, if all adults have constant survival probability s, then adult lifespan D has a geometric distribution with variance $s(1-s)^{-2}$. We will write $Var(D|s)$ to denote this conditional variance given the trait value, and $Var(D)$ to denote the population variance of adult lifespan, which will depend on the distribution of s in the population.

Analysis of the Two-stage Models

Partitioning $Var(LRS)$: Small Trait-variance Approximation

Eq. 1 breaks the variance of LRS into a contribution from luck, which we will call $V_{\mathbb{L}}$, and a contribution from trait variation, which we will call $V_{\mathbb{T}}$. We are interested in learning how much of the variance in LRS is contributed by trait variation: how large is $V_{\mathbb{T}}/(V_{\mathbb{T}}+V_{\mathbb{L}})$?

To get the most from analytic results we assume that trait variation is small with respect to the trait mean — i.e., the trait coefficient of variation (CV) is well below 1. That is, we consider the demographic traits in our models to be functions of an underlying trait x with small variance, $x = \bar{x} + \sigma Z$ where $\mathbb{E}(Z) = 0, Var(Z) = 1$ and σ is treated as a small parameter. Our analytic

approach is to Taylor-expand $V_{\mathbb{T}}/(V_{\mathbb{T}}+V_{\mathbb{L}})$ to leading order in trait variance, express the result in terms of trait CV, and analyze how the leading-order term depends on life-history parameters.

It might seem that we are pre-determining the outcome by using a small-variance approximation. Indeed, in principle the contribution of trait variance to LRS variance can be anywhere from 0 to 100%, if we are free to choose the life cycle, trait variance, and all other model parameters at will. Our already-announced conclusions about the importance of luck are statements about our empirical case studies, and about our simple analytic models within empirically-based limits on parameters. In recent decades we have learned that selection is often strong (Endler, 1986) – some individuals in a population have much higher expected fitness than others – and the evolutionary response can be fast (e.g. Hendry, 2017; Hendry and Kinnison, 1999; Thompson, 1998, 2013). But *strong* and *fast* are relative to the era when a 5% fitness differential would have been called strong selection, and 7-14% change in honeyeater body mass over 300 years was called "rapid evolution" in this journal (Diamond et al., 1989).

The Kingsolver et al. (2012) meta-analysis of studies on phenotypic selection provides a quantitative summary of the amount of standing trait-related fitness variation. They reported that values of the standardized linear selection gradient $|\beta|$ (defined below) on individual fitness components follow an exponential distribution with a median of ≈ 0.16 for cases where directional selection was detected, and that stabilizing selection on individual traits was rarely detected. Selection via differential mating success and fecundity was, on average, stronger than selection via differential survival (Kingsolver et al., 2012, Table S1). The selection gradient is the regression coefficient for relative fitness (or relative fitness component, e.g. clutch size over mean clutch size) as a function of the focal trait, controlling for effects of correlation with other traits; *standardized* means that the coefficient is divided by the trait standard deviation, or equivalently that the trait has been standardized to have variance 1. That is, if z is the trait standardized to have mean 0 and variance 1, and θ is expected fitness (or a fitness component) as function of the trait value, for linear directional selection we have $\theta(z) = \theta(0)(1+\beta z)$ and hence $CV_\theta = |\beta|$. A CV of 20% (i.e., $|\beta| = 0.2$) is at the 58^{th} percentile of the Kingsolver et al. (2012) estimated distribution of $|\beta|$ values, and a CV of 30% is at the 73^{rd} percentile. Thus, the empirical evidence suggests that our small-CV approximation is reasonable for the majority of real-world examples. Moreover, our numerical examples for the two-stage models do not use the small-CV assumption (see archived code `RpartitionItero.R, RpartitionSemel.R` for the full expressions for $V_{\mathbb{T}}/(V_{\mathbb{T}}+V_{\mathbb{L}})$).

It is important to realize that a "small" CV can still entail substantial trait variation. As an illustration, a positive Gaussian distribution[3] with 30% CV has a three-fold ratio between the 95^{th} and 5^{th} percentiles, and even a 20% CV implies a nearly two-fold ratio between the 95^{th} and 5^{th} percentiles.

Partitioning $Var(LRS)$: Results

Our main result for the two-stage models is that, barring unreasonable levels of trait variation, the variance of LRS is dominated by luck in most circumstances. Figs. 1 and 2 show results for between-individual variation in expected annual offspring number F, for the iteroparous and semelparous life histories, respectively, without assuming small trait variance. Figs. S2–S4 in the Supplemental Information show results for variation in adult lifespan, survival to adulthood,

[3] Any Gaussian distribution includes negative values; what we mean is a Gaussian such that negative values are extremely unlikely

and the probability of reproducing before dying (for the semelparous life history). In all cases, the contribution of trait variation is generally modest relative to the effect of luck on LRS.

We can get further insight from the small trait-variance approximation discussed above. The analysis is presented in online Appendix A. For the iteroparous model we find that

$$\frac{V_{\mathbb{T}}}{V_{\mathbb{T}}+V_{\mathbb{L}}} \approx \frac{V_{\mathbb{T}}(\sigma)}{V_{\mathbb{L}}(\sigma=0)} \approx \frac{\bar{s}_J}{CV^2(C_i|\overline{F})/\overline{L}+CV^2(D|\overline{L})+(1-\bar{s}_J)}\Big[CV^2_{s_J}+CV^2_L+CV^2_F + 2CC^2(s_J,L)+2CC^2(s_J,F)+2CC^2(L,F)\Big], \quad (3)$$

where CC denotes the coefficient of covariation, defined by $CC^2(X,Y)=Cov(X,Y)/(\mathbb{E}(X)\,\mathbb{E}(Y))$ and an overbar denotes the population average (see Table 1). For the semelparous model,

$$\begin{aligned}\frac{V_{\mathbb{T}}}{V_{\mathbb{T}}+V_{\mathbb{L}}} \approx & \left[\frac{1}{\left(\frac{\overline{d}}{\bar{s}_J\overline{b}}+\frac{1-\bar{s}_J}{\bar{s}_J}\right)\left(1+CV^2(C|\overline{F})\right)+CV^2(C_i|\overline{F})}\right]\times \\ & \Big[CV^2_F+CV^2_{s_J}+\frac{\overline{d}^2}{(\overline{d}+\overline{b})^2}(CV^2_b+CV^2_d) \\ & +\frac{2}{\bar{s}_J\overline{F}}CC^2(s_j,F)+2\frac{\overline{d}}{\bar{s}_J\overline{b}(\overline{b}+\overline{d})}CC^2(s_j,b)-\frac{2}{\bar{s}_J(\overline{b}+\overline{d})}CC^2(s_j,d) \\ & +2\frac{\overline{d}}{\overline{b}\,\overline{F}(\overline{b}+\overline{d})}CC^2(F,b)-\frac{2}{\overline{F}(\overline{b}+\overline{d})}CC^2(F,d)-2\frac{\overline{d}}{\overline{b}(\overline{b}+\overline{d})^2}CC^2(b,d)\Big].\end{aligned} \quad (4)$$

Examining these equations, we see that trait variation can only make a large contribution to LRS variance if it is not opposed too much by negative co-variation among different fitness components (the CC^2 terms). Large negative CC terms would be expected in the presence of life history tradeoffs, for example if (in either model) high juvenile survival is achieved by maturation at a small size that entails higher annual mortality as an adult, and lower expected fecundity at each breeding attempt.

We can also see that the only way to make the relative contribution of trait variation substantial is to restrict the potential contributions of luck. For example, for both iteroparous and semelparous life histories, the relative importance of trait variation increases as offspring number becomes less variable (eqs. 3 and 4 decrease with $CV^2(C|\overline{F})$.) Similarly, the relative contribution of trait variation increases as adult lifespan (and thus the number of reproductive bouts) becomes less variable for iteroparous life histories (eq. 3 decreases with $CV^2(D|\overline{L})$).

Organisms must also survive long enough to reproduce in order for trait variation to affect LRS. For both iteroparous and semelparous life histories, the relative contribution of trait variation increases with survival to adulthood, s_J. Increasing s_J can also be viewed as a means of damping the contributions of luck: $V_{\mathbb{L}}(\sigma=0)$ includes a term $R_0^2(1-s_J)/s_J$, where R_0 is the expected LRS, so $V_{\mathbb{L}}$ becomes large as s_J becomes small. Along the same line, if expected offspring number (F) and/or survival to adulthood (s_J) are the variable traits in a semelparous life history, then trait variation is only important if individuals are likely to reproduce before dying ($\overline{b}>\overline{d}$).

(However, the relative contribution of trait variation is non-monotonic in $\overline{b}$ and $\overline{d}$ if b or d are varying.)

For iteroparous life histories, the effect of expected adult lifespan depends on how the coefficient of variation of lifespan depends on expected lifespan: in eq. 3, the denominator contains the term $\left(CV^2(C|\overline{F})/\overline{L} + CV^2(D|\overline{L})\right)$, which depends on $\overline{L}$ in different ways depending on the distribution of adult lifespan. For example, if adult lifespan is normally distributed with variance σ_L^2 (not depending on $\overline{L}$), the term in parentheses becomes $CV^2(C|\overline{F})/\overline{L} + \sigma_L^2/\overline{L}^2$, and the relative contribution of trait variation increases as $\overline{L}$ increases. On the other hand, if adults survive each year with probability s (geometrically-distributed lifetime), then $CV^2(D|\overline{L}) = 1 - 1/\overline{L}$. The term in parentheses becomes $CV^2(C|\overline{F})/\overline{L} + 1 - 1/\overline{L}$, and the relative contribution of trait variation can increase or decrease with $\overline{L}$, depending on the magnitude of $CV^2(C|\overline{F})$. However, whether $CV^2(D)$ declines or increases with L is not determined by the shape of the survivorship curve.

We can consider annual life histories by choosing a fixed lifespan of 1 year and setting $s_J = 1$ in the iteroparous two-stage model. This leaves mean annual offspring number as the only potentially varying trait. Fig. 1 shows that with a Poisson clutch size and fixed lifespan, trait variation contributes more in perennial organisms than in annuals. With $L = 1$, $s_J = 1$, trait variation contributes only 15% of the variance of LRS.

As we reduce opportunities for luck (by letting s_J approach 1, assuming constant clutch size, and, in our iteroparous two-stage model, assuming constant lifespan conditional on trait value), the contribution of trait variation will eventually exceed that of luck. However, even with high trait variation ($CV = 0.3$, a roughly 3-fold ratio between the 95th and 5th percentiles of expected annual fecundity), the contribution of trait variation is at most 25% of the total variance in LRS unless survival to adulthood is 80% or better (top-left panel of fig. 1).

Predicting Traits from LRS: Method

We chose expected offspring number, F, as the focal trait (though any other could have been chosen instead), and in our numerical examples we assumed that it had a Gaussian distribution. If an individual lives to reproduce D times (adult lifespan D), then its LRS is the random variable $R = \sum_{i=1}^{D} C_i$, where C_i is its output in the ith reproductive bout. The sum of a fixed number of independent Poisson random variables also has a Poisson distribution. This means that if offspring number is Poisson distributed with mean F ($C_i \sim \text{Pois}(F)$), then the distribution of LRS conditional on D is Poisson with mean DF ($R \sim \text{Pois}(DF)$).

For a fixed adult lifespan L, the sum of reproductive outputs consists of precisely L terms, so LRS is Poisson distributed with mean LF: $\Pr(R|F) = \text{Pois}(R|LF)$, where $\text{Pois}(R|LF)$ is the probability of outcome R for a Poisson distribution with mean LF. Thus,

$$\Pr(F|LRS = R) = \frac{\Pr(R|F)\Pr(F)}{\sum_F \Pr(R|F)\Pr(F)} = \frac{\text{Pois}(R|LF)\Pr(F)}{\sum_F \text{Pois}(R|LF)\Pr(F)}. \tag{5}$$

If adult lifespan is variable, then $\Pr(R|F) = \sum_D \text{Pois}(R, FD)\Pr(D)$. Thus,

$$\Pr(F|LRS = R) = \frac{\Pr(F)\sum_D \text{Pois}(R, DF)\Pr(D)}{\sum_F \Pr(F)\sum_D \text{Pois}(R, DF)\Pr(D)}. \tag{6}$$

Inferring traits from LRS: Results

The strong influence of luck is also seen when we try to predict traits from observed LRS. For a population with Gaussian between-individual variation in expected offspring number F, fig. 3 shows the conditional probability of the trait value given observed LRS. If all adults have exactly the same lifetime, the contribution of luck is suppressed enough that there is a clear relationship between LRS and trait: those with above-average lifetime productivity probably have above-average expected offspring number, although even those in the 90th percentile of LRS are only expected to have a value of F about one standard deviation above the population average. However, if adult lifetime is variable, this relationship is almost completely washed out. The most likely trait value varies only weakly with LRS, and the uncertainty about this value is large. The most likely trait value for those in the 90^{th} percentile of LRS is less than half a standard deviation above the population average, and there is a substantial probability that even these exceptionally productive individuals had a trait value below the population average.

Prototype size-structured model

Is the surprisingly high importance of luck in the two-stage models an unintended side-effect of assuming simple life cycles with just two discrete stages? To partially address that question we jump to the opposite extreme, continuous size variation in an integral projection model (IPM) similar to many in the recent literature. Because the results for this model align closely with those for the two-stage models, we keep this section very brief; most of the information is in online Appendix B.

Emulating published IPMs we used a log-transformed size measure (e.g., size is log(total leaf area)), modeled survival as a logistic regression on size, growth as a linear regression on size, and fecundity as zero below a critical size and then increasing linearly with increasing size. A single individual trait ("quality") potentially affects size at birth and size-dependent growth, survival, and fecundity. We considered two baseline parameter sets (Table B1) giving relatively short expected lifespan with high per-capita annual fecundity, versus longer life with lower annual fecundity. Fig. B1 shows the demographic functions for the two parameter sets.

For each baseline set, the LRS variance decomposition and other life-cycle properties were calculated for 250 random parameter sets generated by perturbing each baseline parameter. The results (figs. B4 and B5) agree with the two-stage model analysis: for realistic levels of variation in traits affecting fitness, trait-dependent variance in LRS can sometimes be a nontrivial fraction of the total variance, but it is typically dominated by chance variation. This pattern again reconciles the apparent conflict of empirical studies where trait-dependent variation in LRS has been detectable (e.g, Cam et al., 2012; Chambert et al., 2013; Hamel et al., 2009; Plard et al., 2015a), with theoretical analyses showing that models without trait variation could largely account for observed variance in LRS (Orzack et al., 2011; Steiner and Tuljapurkar, 2012; Tuljapurkar et al., 2009).

Empirical Case Studies

We now apply our approach to two empirical case studies. The first is an extension of the previously published age- and breeding stage-structured model of kittiwakes (*Rissa tridactyla*),

a long-lived seagull (Steiner et al., 2010). The second involves size- and competition-structured integral projection models of two perennial plants, the shrub *Artemisia tridentata* and the perennial grass, *Pseudoroegneria spicata* in Idaho (USA) sagebrush steppe (Adler et al., 2010), using the models developed online Appendix C.

Kittiwakes

Partitioning $Var(LRS)$

We use the stage- and age-classified matrix model for female kittiwakes from Steiner et al. (2010). Individuals are classified as immature, non-breeders, failed breeders (i.e., breeders that fledge no chicks), breeders that fledge one chick, and breeders that fledge two or three chicks. The matrix for transitions among these stages is age-dependent, with separate matrices estimated for ages 1, 2, 3, 4, and 5 or older.

Following Cam et al. (2002), we let adult survival and breeding probability positively co-vary among individuals. We make the conservative assumption that survival and breeding probability are both functions of an underlying "quality" variable x, so that survival and breeding probability are perfectly correlated. According to eq. (3), perfect correlation should maximize the relative importance of trait variation.

For the kittiwake model, the distribution of LRS depends on quality x and state z (a combination of age and reproductive stage). Using the methods of Ellner et al. (2016, Ch. 3), for any x we can calculate $\mathbb{E}(R|z)$ and $Var(R|z)$ as functions of z, thus obtaining $\mathbb{E}(R|x,z)$ and $Var(R|x,z)$ as functions of (x,z). We are interested in the accumulation of offspring from birth to death, and all kittiwake chicks are born into the same state z_0 =(immature, age 1). We can then compute the terms in eq. 1 using

$$Var(R|x) = Var(R|x,z_0) \quad \mathbb{E}(R|x) = \mathbb{E}(R|x,z_0). \tag{7}$$

These calculations are carried out in online SI file `KittiwakeVarPartitionTable.R`.

Based on (Cam et al., 2002), we take the survival CV to be 0.2, with a breeding probability CV of 0.03. The table below shows that even assuming perfect correlation in survival and breeding probability, luck has a very large influence on both LRS and lifespan: trait variation contributes only 38.9% of the variation in LRS and 33.7% of the variation in lifespan:

	Var(LRS)	Var(Lifespan)
Percentage from trait variation	38.9%	33.7%

Inferring traits from LRS

We calculated $\Pr(R|x)$ numerically by first extending the model to include cumulative offspring production to date as an additional individual state variable; Snyder and Ellner (2016) call this a "size-kids" model because individuals are cross-classified by current size and by how many kids they have had so far during their life. We then calculate the state-at-death distribution for the extended model (Ellner et al., 2016, Chapter 3), for a finely-spaced set of x values. Because R is the number of kids "so far" at the moment of death, its distribution is implied by the state-at-death distribution of the extended model (Ellner et al., 2016, Chapter 3).

The dominant role of luck in kittiwake LRS also makes it difficult to infer individual quality from individual LRS (fig. 4). Most individuals never have offspring, so those in the 25^{th} to

75^{th} percentile of LRS most likely have nearly average survival and breeding probability (i.e., the conditional probability distribution for quality given LRS is centered more or less at the population average quality.) It is nearly impossible to be in the top 10% of LRS without having above-average quality (the conditional probability distribution for x given high LRS is almost entirely above the population mean of x). However, above-average quality is no guarantee of reproductive success (i.e., for individuals with low LRS, the trait distribution conditional on LRS extends well above the average trait value). In short, having exceptionally good survival rate and breeding probability are necessary but not sufficient for having exceptional LRS: luck is also required[4].

Our two-stage model with iteroparity offers some insight into the results for kittiwakes. Although kittiwake offspring number is not especially variable, adult lifespan is. Most individuals reach age 5 or older (an average quality individual has a 95% probability of reaching at least age 5), at which point they have a constant survival probability per year (because ages 5 and older are grouped in the model). The constant survival probability means that adult lifespan is geometrically distributed, with CV = survival probability = 0.81 for an average quality individual. This is considerably larger than the CVs for between-individual variation in survival or breeding probability. Thus, much of luck's sway can be attributed to the large variation in kittiwake adult lifespans.

Perennial plants

Partitioning $\boldsymbol{Var}(LRS)$

The perennial plant models (described in detail in online Appendix C) are empirically parameterized size-structured IPMs with a mean field approximation for neighborhood competition. They are very similar to the previously published models for those species (Adler et al., 2010; Chu and Adler, 2015), except that here seedlings are a separate life stage with all seedlings having the same size (in the original data, they were mostly recorded as too small to measure). The individual trait x in these models is W_1, the intensity of neighborhood competition in the year of birth (age 1), which depends on where the seedling is located. Competition W_1 affects the individual's probability of survival to age 2, $s(W_1)$, and the intensity of competition at age 2 if it survives, W_2. Competition W_2 and the individual's size at age 2, Z (which is not affected by W_1) then determine the distribution of lifetime reproductive success R conditional on survival to age 2. While it is possible (and likely) that traits besides competition at birth vary among individuals and affect their expected LRS, we focus here on this one trait because, as explained in the Introduction, our intuition suggested that it would be a critical factor in LRS variation.

For the analyses here, the key issue is how well the new seedling survival model predicts the association between W_1 and survival. We can test this by comparing the observed and predicted distributions of W_1 values among seedlings that survive to age 2; these are plotted in online SI figs. C1 - C4. For *Artemisia* the mortality at higher W values may be slightly over-estimated, though it is hard to be sure because the number of surviving recruits is so small; otherwise there is a very close match between the observed and predicted distributions.

[4]Similar conclusions have been reached about human economic success (Frank, 2016).

In Supplemental Information section *Analysis of partitioning by W in the perennial plant IPMs* we derive the partitioning

$$\begin{aligned} Var(R) = &\underbrace{\mathbb{E}_{W_1,Z}[s(W_1)\, Var(R^*|W_1,Z)]}_{①} + \underbrace{\mathbb{E}_{W_1,Z}[s(W_1)(1-s(W_1))(\mathbb{E}(R^*|W_1,Z))^2]}_{②} \\ &+ \underbrace{\mathbb{E}_{W_1}[s(W_1)^2\, Var_Z\, E(R^*|W_1,Z)]}_{③} + \underbrace{Var_{W_1}[\mathbb{E}(R|W_1)]}_{④}, \end{aligned} \tag{8}$$

where R^* is lifetime reproductive success conditional on surviving to age 2, and we explain how each term can be calculated numerically. Term ④ is the trait variation term, the main effect of W_1 on LRS. It includes the immediate effect of W_1 on survival to age 2 and the delayed effects of W_1 on neighborhood competition later in life, which occur because neighborhood composition changes gradually over time and which affect survival and growth of older plants.

The other terms are different components of luck – variation in LRS unrelated to W_1. Term ② is the contribution to LRS variance from survival or not to age 2. Term ① is average variance in LRS among survivors, above and beyond the variance due to differences in their W_1 and Z values. It is variance resulting from the fact that reproductive success is not a deterministic function of Z and W_1. Term ③ is the average variance in LRS due to variation in size at age 2 of survivors. This can be considered as a trait variation term rather than luck, if Z is regarded as a second individual-level trait in addition to W_1.

Using the models to project the fate of a seedling cohort (figs. 5 and 6) shows that, as expected, initial site quality W_1 has a very large effect on a seedling's chances of surviving to reach full adult size. One reason for this is that site quality does not change very rapidly, so that the initial high variability in annual survival rate persists for several years. The dashed blue lines in figs. 5B and 6B highlight the wide range of annual survival rates at ages 2 and 3, among individuals who have survived to that age. In contrast, initial site quality has little effect on the growth or fecundity of survivors, in both species (figs. 5C, D and 6C, D).

Despite the large impact of W_1 on survival, the contribution of variation in W_1 to variation in LRS is very small (Table 2). The two terms in the partition (8) that could be viewed as trait variation (initial site quality ④, and size at age 2 ③) are under 2% of the total variance in both species. Survival (or not) to age 2 unrelated to site quality is a less inconsequential component of the variance in LRS, but by far the largest component in both species is term ①, the variation in life trajectories from age 2 onwards that is unrelated to initial site quality or initial size.

Only a small part of this variation is due to variation in offspring number, either chance variation or size-dependent variation. We repeated the calculation of the four terms under the assumption that all individuals age 2 or above produce exactly the same number of recruits in each year of life, obtaining the values in square brackets in Table 2. Variation in LRS is still dominated by the variation from age 2 onwards unrelated to variation in W_1, which (in these calculations) is entirely due to variation in lifespan.

Again, the two-stage model with iteroparity helps us to understand this outcome. Adult lifespan in the perennial plants is highly variable because individuals who make it past the first few years have low and relatively stable annual mortality thereafter, leading to a geometric lifetime distribution (figs. 5B and 6B). The perennial plants are essentially in the situation of the middle panels of fig. 1. Unless adult lifespan is relatively constant, or the trait value is highly

predictive of adult lifespan, trait-driven variance in LRS is dominated by the effect of adult lifespan variability.

Inferring traits from LRS

The size-kids classification that we used for the kittiwakes becomes computationally infeasible for the perennial plants because it would require a three-way classification (size, neighborhood competition W, and offspring to date), producing a prohibitively large transition matrix. However, we found (figs. B2 and B3) that the focal trait (competition at birth, W_1) mainly affects survival, and conditional on survival, expected growth and annual fecundity are nearly independent of W_1. So as in other long-lived plants, high LRS is mostly a matter of surviving to reproduce many times (Snyder and Ellner, 2016). We can therefore use lifespan as a surrogate for LRS and ask: did the longest-lived individuals necessarily experience low competition as a seedling? Moreover, because it is rarely possible to associate a new recruit with a specific parent, this relationship is also the prediction that could be tested in long-term data by asking if large and therefore old individuals necessarily experienced low crowding early in life. The calculations are eq. (2) with $x = W_1$ and lifespan L in place of R. The conditional probability $\Pr(L|W_1 = w)$ can be computed by simulating a cohort of recruits with initial neighborhood crowding w, and recording the number that die at each age; $\Pr(W_1)$ is the empirical estimate of the frequency distribution of initial neighborhood competition; and $\Pr(L)$ can be computed by simulating a cohort of recruits with W_1 drawn from the distribution $\Pr(W_1)$.

The distributions of W_1 given lifespan L are shown in figs. 7 and 8. In both plant species, as in kittwakes, trait value and eventual success are not tightly coupled. The most long-lived individuals generally had better than average (i.e. smaller than average) initial crowding W_1, though not by much (roughly half a standard deviation below the mean crowding experienced by all seedlings, panels B). Many individuals at the low end of the lifespan distribution had better than median initial crowding W_1, while a substantial fraction ($\approx 20\%$) at the high end had worse than median initial crowding (panels C). So for the perennial plants, despite the large effect of initial crowding on survival to age 2, starting life in a good location is neither necessary nor sufficient for becoming one of the large, lucky few who live long and reproduce often.

Selection

Given that variation in reproductive success is dominated by luck, one might begin to wonder what the implications are for selection. The important thing to remember is that the processes underlying selection (births and deaths) occur at the individual level, while evolutionary change is observed at the population level – a change in allele or trait frequencies. For a large enough population, variation in offspring number due to luck will average out over individuals with similar trait values. Thus, at the population level, luck may average out, allowing trait variation to shine through.

Following the approach of Rice (2008), we calculate the expected change in population average trait value over one annual time step ($\mathbb{E}\,\Delta\bar{x}$), accounting for the contributions of luck. We assume that the trait x has a distribution with mean $\bar{x}$ and a small variance, and that offspring have the same trait as their parent (asexual reproduction with perfect heritability). In Supplemental

Information section *Quantifying selection when fitness is a random variable* we show that

$$\mathbb{E}\,\Delta\bar{x} \approx \frac{\widehat{w}'(\bar{x})}{A}\,Var(x)\left(1+\frac{1}{A^2N}\,Var(w|x)\right), \tag{9}$$

$$Var\,\Delta\bar{x} \approx \frac{Var(w|x)\,Var(x)}{A^2N}, \tag{10}$$

where N is the population size, $\widehat{w}(x)$ is the expected yearly offspring number for an individual with trait x, $A = \widehat{w}(\bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})\,Var(x)$ is an approximation of the expected yearly offspring number averaged over trait variation, and $Var(w|x)$ is the variance of the yearly offspring number around $\widehat{w}(x)$ (the equivalent, for w, of the "luck" term in eq. (1)).

The first term in eq. 9 is very similar to the usual expression for the change in mean trait value (Iwasa et al., 1991, eq. (A6)): the change is the product of the relative *expected* fitness gradient ($\widehat{w}'(\bar{x})/A$) and the trait variance ($Var(x)$). $\widehat{w}'(\bar{x})\,Var(x)$ is the first-order approximation to the among-individual variance in $\widehat{w}(x)$, so expected trait change is proportional to the variance among individuals of expected fitness given their trait (the equivalent for w of the "trait variation" term in eq. (1)). Luck in reproductive success, measured by $Var(w|x)$, has an effect on expected trait change that is inversely proportional to population size, because of the averaging of luck across individuals with similar traits. Similarly, the "random drift" component of trait change, eq. (10), is proportional to $Var(w|x)/N$ and decreases as luck is averaged across more individuals.

Can luck play a role in selection when populations are not small? Constable et al. (2016) have shown that luck may be important in weakly-coupled metapopulations with small local populations. But there may be other ways. Eqs. (9) and (10) also apply to trait change from one generation to the next, with w given by LRS. As an example, motivated by our two-stage and empirical models, suppose that the chance variation in LRS is the result of a two-stage process: individuals survive to maturity with probability s_J, and conditional on survival have (random) LRS Z with mean $1/s_J$ so that population size is stable (i.e., LRS is $R = BZ$ where B is a 0-1 random variable with $Pr(B=1) = s_J$, and $\mathbb{E}\,Z = 1/s_J$). We then have $A \approx 1$, and using eq. (A7) we have

$$\frac{Var(w|x)}{N} = \frac{1 - s_J + CV_Z^2}{s_J N}. \tag{11}$$

(If s_J or CV_Z vary among individuals, this would hold as an approximation using typical values of s_J and CV_Z). The denominator in (11), $s_J N$, is an effective population size, the number that potentially contribute to the next generation. Absent luck in adult LRS (e.g., if every adult survives to breed once and has $1/s_J$ offspring), CV_Z is zero and the numerator in (11) would be $1 - s_J < 1$. In several of the examples in this paper, the distribution of Z is approximately exponential. An exponential distribution has $CV_Z = 1$, so the random variation in adult LRS more than doubles the value of (11).[5] However, with a fatter-tailed distribution of adult LRS, CV_Z can be arbitrarily large, so that effects of luck could persist at very large population sizes. For example, a power-law distribution with finite variance ($Pr(Z=z) = (1+z)^{-k}, z > 0, k > 3$) has $CV_Z^2 = (k-1)/(k-3)$. The effects of luck in adult LRS on the mean and variance of trait change are then inversely proportional to $s_J N(k-3)/(k-1)$ which can be far smaller than the population size N.

[5] If trait variation causes s_J or CV_Z to vary among individuals, this would be a statement about an average individual.

Discussion

We have found that lifetime reproductive success is often governed largely by luck. Individuals within a population frequently differ from one another in ways that affect their expected success, but actual outcomes are commonly so variable, with or without trait variation, that unless the effects of luck are substantially restricted (e.g. by fixing reproductive lifespan), the additional effects of trait variation between individuals are difficult to detect. This remains true regardless of which property varies among individuals (expected offspring number, adult lifespan, survival to adulthood, etc.), and regardless of life history type (iteroparous or semelparous) for our general models and for all of our empirical case studies.

In addition to contributing most of the variability in LRS, luck also obscures the relationship between LRS and individual traits. In our empirical examples (a long-lived seagull, a shrub, and a perennial grass), having exceptionally good traits is not sufficient to guarantee exceptionally high LRS. And in some cases, it isn't even necessary. In theory the link can be tight, so that individuals with very low LRS are nearly certain to have below-average traits (e.g., fig. 3A). But this situation is only likely in real populations that do not have much reproductive skew. If the distribution of LRS is skewed so that only a "lucky few" individuals dominate offspring production, any genotype so unfit that an individual with that genotype has no chance of becoming one of the lucky few will quickly be removed by natural selection. That is, natural selection will limit trait variation to a point at which even those with the least-beneficial trait values may still have offspring (apart from recent and therefore rare deleterious mutations), so that the link between LRS and trait value is blurred. We therefore predict that a tight link between trait values and LRS will rarely be observed in populations with substantial reproductive skew.

Variability due to luck has some intuitive sources. Luck tends to swamp the contributions of trait variation as the number of offspring per reproductive bout becomes more variable (specifically, as the coefficient of variation increases) or, for iteroparous life histories, as the CV of adult lifespan increases. In all of our empirical examples, variability in adult lifespan is a large source of variability due to luck. Variability in LRS will also be due largely to luck if few individuals survive long enough to reproduce, or if negative tradeoffs among fitness components constrain individuals to have similar expected LRS, despite large variation in several traits that affect fitness.

Because lifespan variation is often a key driver of variation in lifetime outcomes, it is important to predict this variation accurately. However, lifespans predicted from demographic models are often a long-term extrapolation from short-term data (year-to-year survival and growth), or from a model in which all individuals beyond some age have the same demographic rates. Analyses of individual stochasticity and its lifetime impacts (e.g., Caswell, 2009, 2011; Orzack et al., 2011; Snyder and Ellner, 2016; Steiner and Tuljapurkar, 2012; Steiner et al., 2010; Tuljapurkar et al., 2009, and this paper) depend on those extrapolations being accurate enough. This should be tested empirically, whenever possible, by comparing observed and predicted lifespan distributions (e.g. Steiner and Tuljapurkar, 2012, fig. 1B).

Our findings indicate that comparing observed variance in LRS with the variance expected in the absence of trait variation will generally not be an effective approach for asking whether trait variation is present in a population. Bonnet and Postma (2016) found that this "null model" approach lacks statistical power in models based on empirical studies of snow vole demography.

Our findings offer an explanation for theirs, and suggest that their conclusions are likely to hold for many organisms, both perennials and annuals.

The methods presented here can be used to examine contributions to variation in other measures of individual success, such as lifespan. In our case studies, luck dominates variation in lifespan also. We have shown that variation in survival and breeding probability contributes only 34% to the variability in lifespan for our kittiwake case study, and for our perennial plant models, little can be inferred about the "traits" (competition at birth) of long-lived individuals.

However, the effects of luck may average out for population measures of success. For example, we show that the expected change in the population average trait value is equal to the usual selection formula plus a correction term incorporating variance due to luck that vanishes as the effective population size becomes large. However, we have only considered effects of trait variation within a single generation. There may be cumulative impacts that accrue over multiple generations even in the absence of evolutionary change in trait distributions. Furthermore, while the correction term for luck vanishes as $1/$ population size, the constant of proportionality may be large in some cases. If luck does play an important role in some population-level measures of success, then a focus on within-species trait variation may not have much power to explain ecological patterns.

In short, while trait variation may influence the fate of populations, it is often the case that luck governs the lives of individuals. In some respects this is good news. It means that null models which ignore individual variation (and are thus spared the effort to quantify variation and its effects) may be acceptably accurate for predicting the variance in individual outcomes and thus the magnitude of demographic stochasticity, which is an important factor in extinction risk and population variability. But it also means that we will rarely, if ever, be able to infer that individual variation is present by rejecting the predictions of null models. To learn about individuals, we need to make repeated direct observations, and analyze the data appropriately (Cam et al., 2016), not reason backward from lifetime measures of success.

Acknowledgements

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Table 1: Summary of notation for the general two-stage models. Suggested mnemonics are indicated by an underlined letter.

Notation	Meaning or formula
R	An individual's (random) lifetime reproductive success: total number of offspring, regardless of when they are born.
V_R	Variance in R, including both luck and trait variation.
$V_{\mathbb{T}}, V_{\mathbb{L}}$	Trait and Luck components of V_R, with $V_R = V_{\mathbb{T}} + V_{\mathbb{L}}$.
s_J	Probability of survival from birth to adulthood.
C_i	Realized offspring number("clutch size") by an individual in year i as an adult. Typically assumed to be either constant or Poisson distributed.
F	$\mathbb{E}[C_i]$, expected annual per-capita fecundity.
σ_C	Standard deviation of offspring number.
D	Adult realized lifespan (age at death, random) – number of years as a mature individual, before death.
L	$\mathbb{E}[D]$, expected adult lifespan.
σ_D	Standard deviation of D.
s	Adult annual survival probability (in models with age-independent adult survival).
b	Semelparous model: adult annual probability of breeding (which is fatal).
d	Semelparous model: adult annual probability of death without breeding.
$\overline{\bullet}$	Average of parameter or trait $\bullet$ across the population (e.g., $\overline{F}$ is the population average of F).

Table 2: The four terms in the general partitioning for the perennial plant IPMs, eq. (8), calculated for *Artemisia tridentata* and *Pseudoroegneria spicata*, expressed as a fraction of the total variance in LRS.

Component of variation in LRS	*Artemisia*		*Pseudoroegneria*	
Initial site quality W_1, ④	0.3%	[0.7%]	0.5%	[0.9%]
Survive to age 2?, ②	12.1%	[25.4%]	12.0%	[19.6%]
Size at age 2, Z_2, ③	1.0%	[1.25%]	1.4%	[1.75%]
Average variance given W_1, Z_2, ①	86.7%	[72.6%]	86.1%	[77.8%]

Note: The terms are listed here in temporal order: seedling (age 1), age 2, and beyond age 2. Values in square brackets are the fractional term values that result from making annual reproduction independent of size and deterministic, so that all individuals age 2 or above produce exactly the same number of new recruits each year.

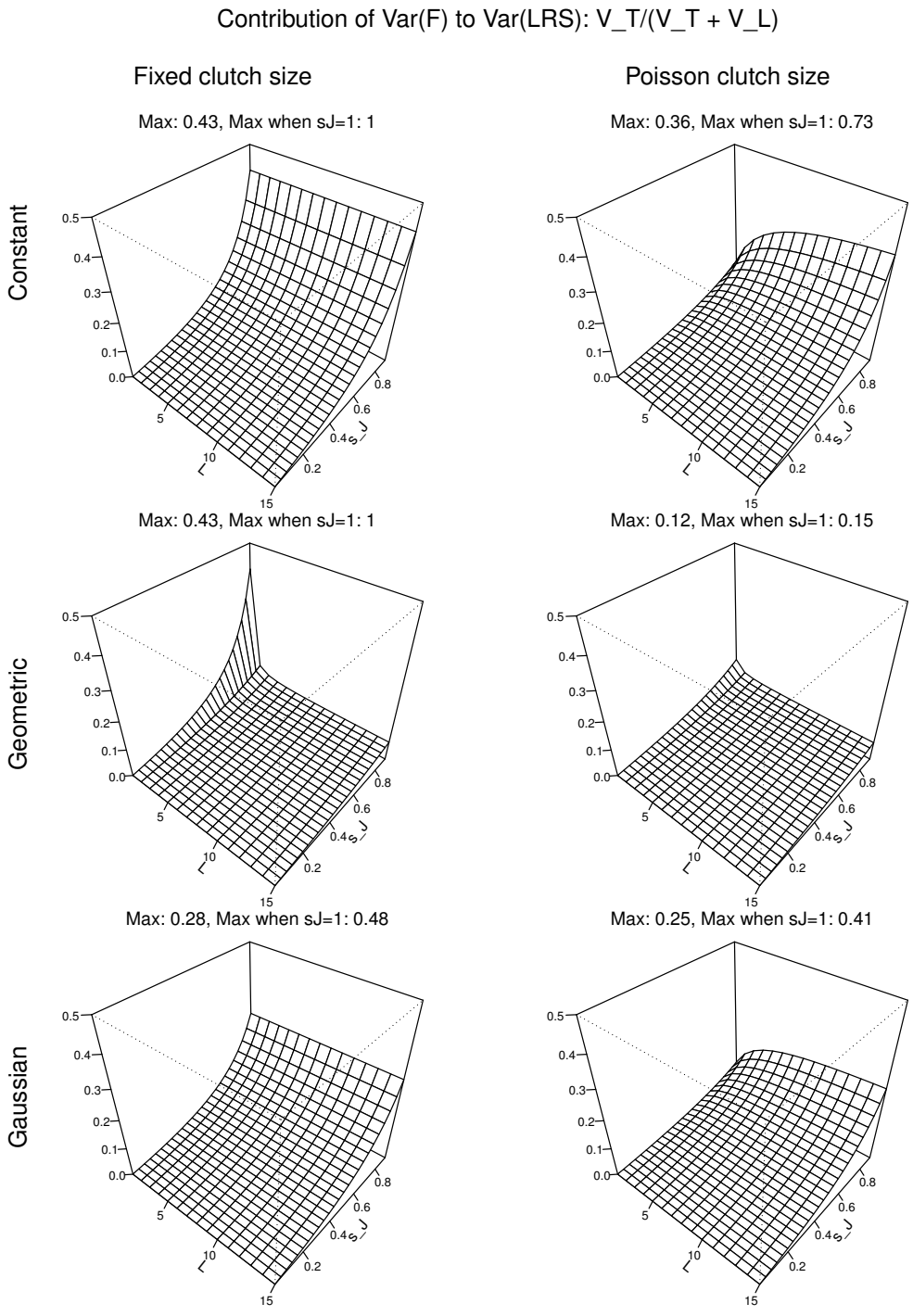


Figure 1: [Figure 1 caption here.]

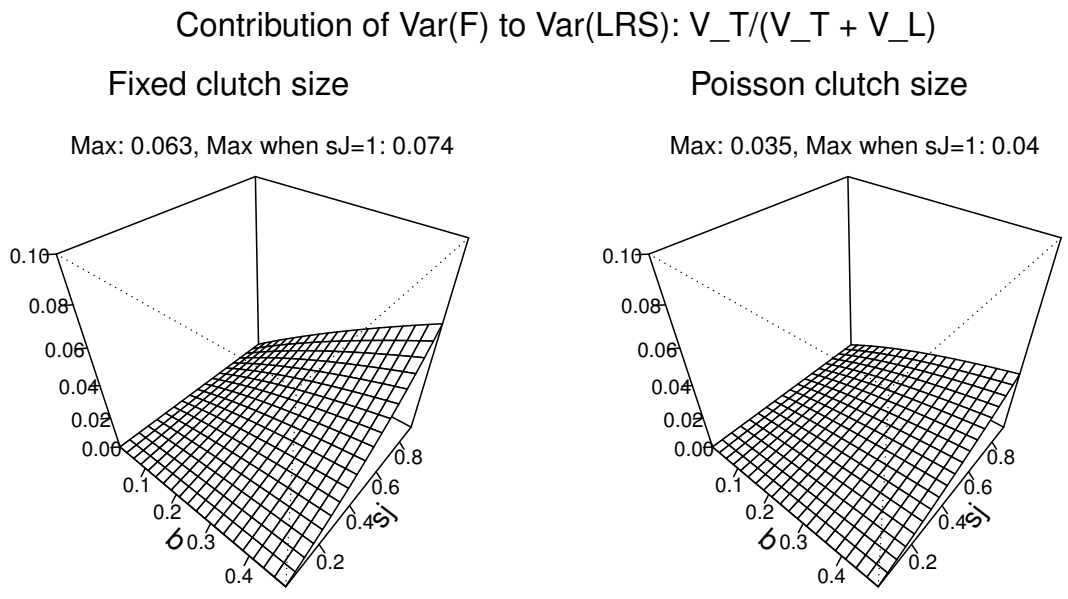
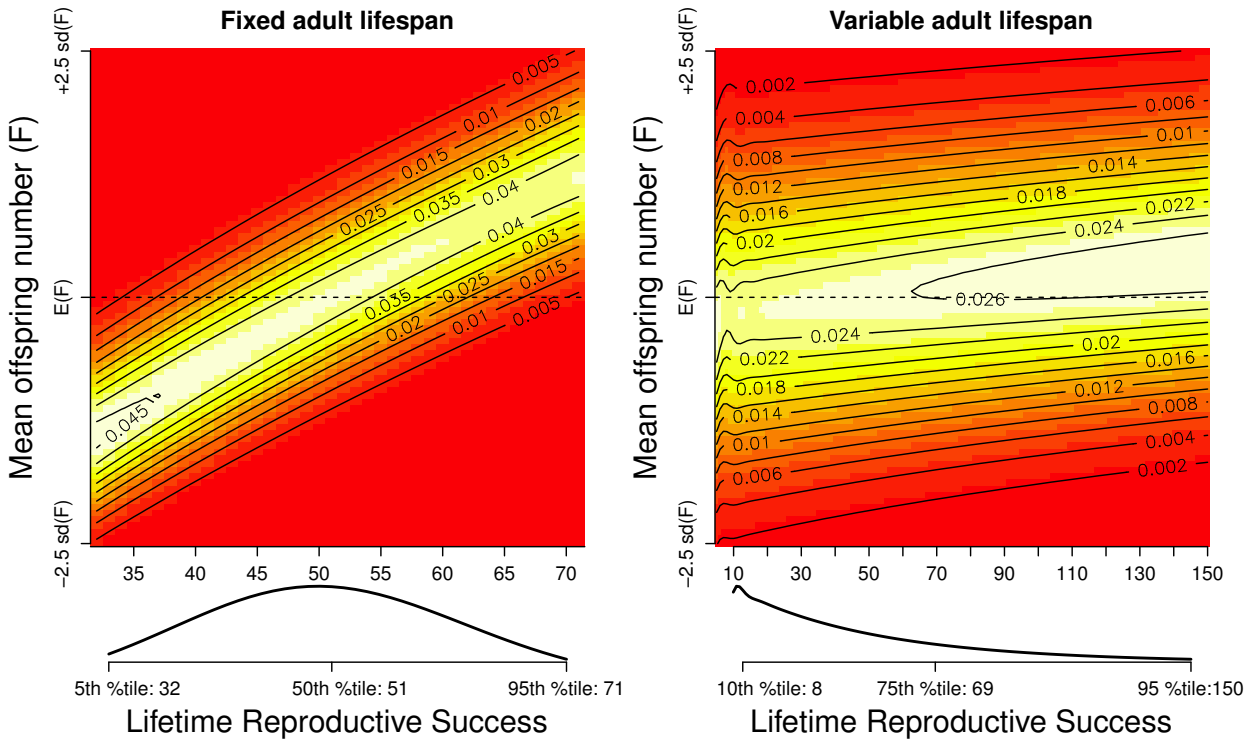


Figure 2: [Figure 2 caption here.]



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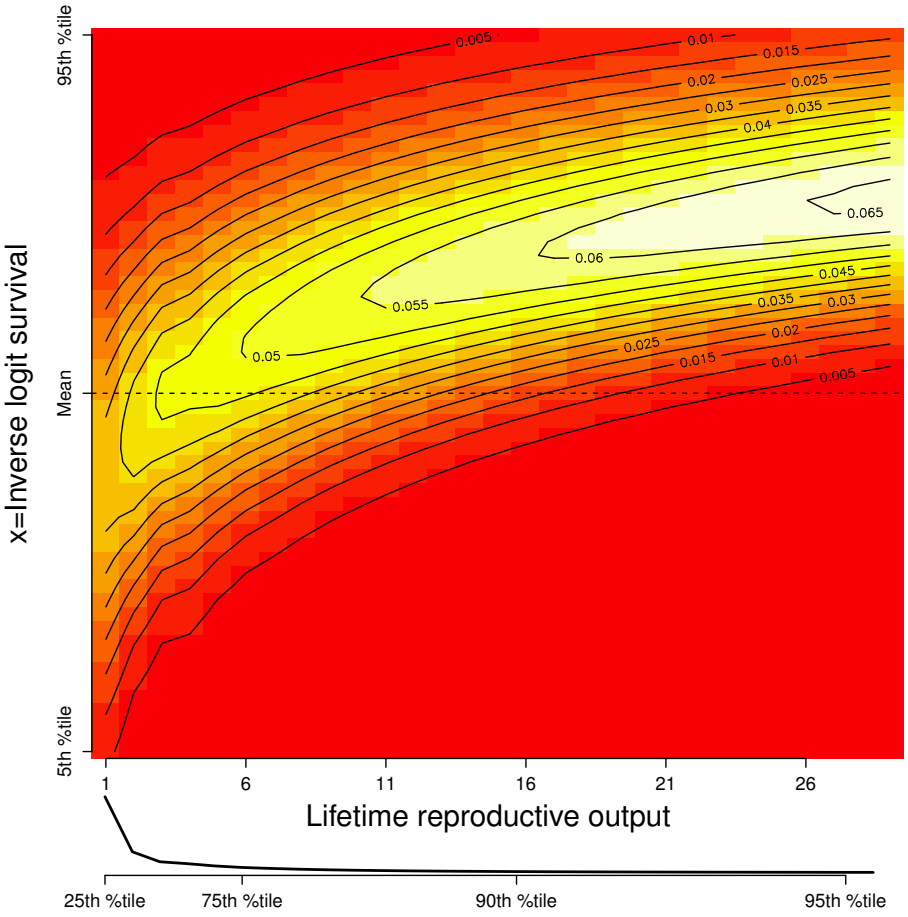

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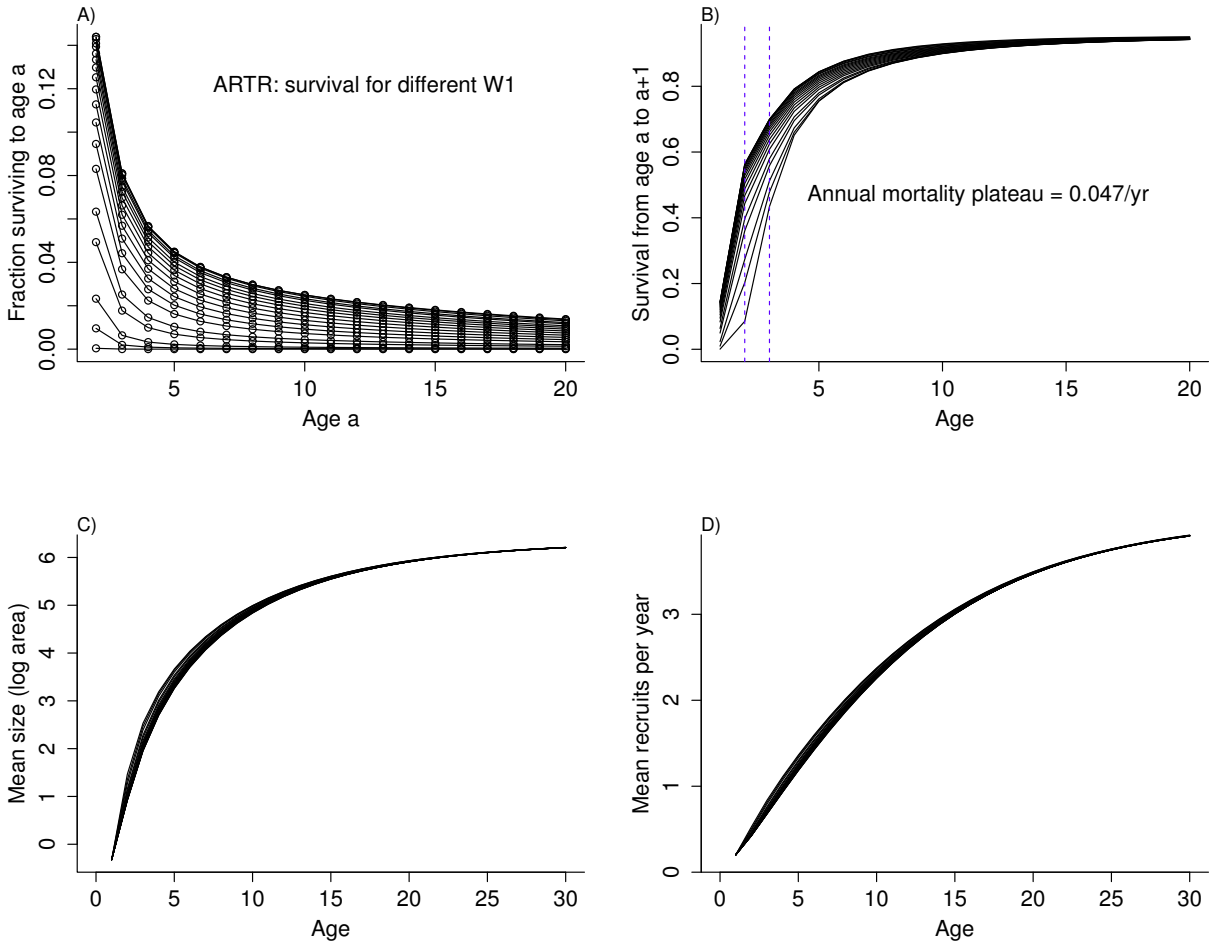

Figure 5: [Figure 5 caption here.]

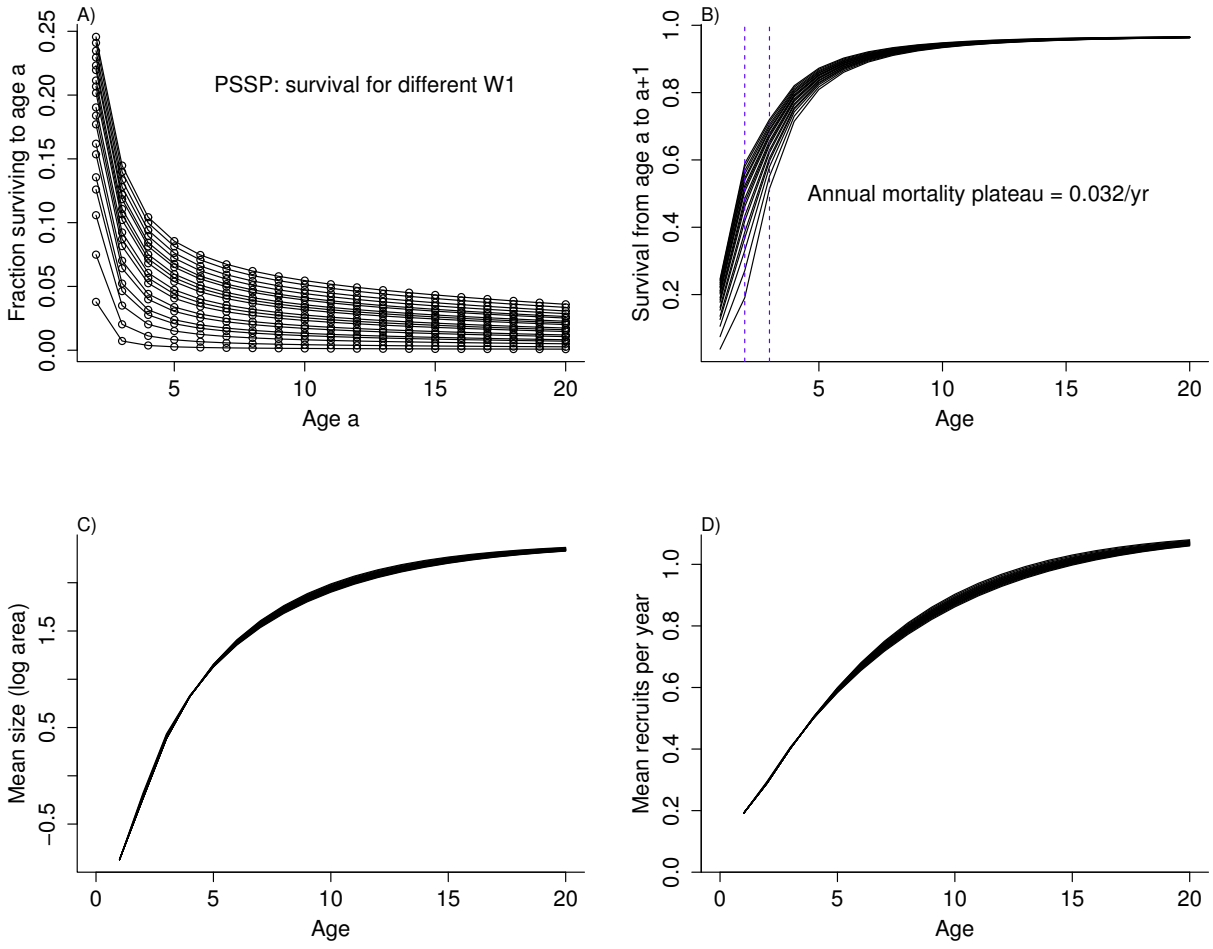

Figure 6: [Figure 6 caption here.]

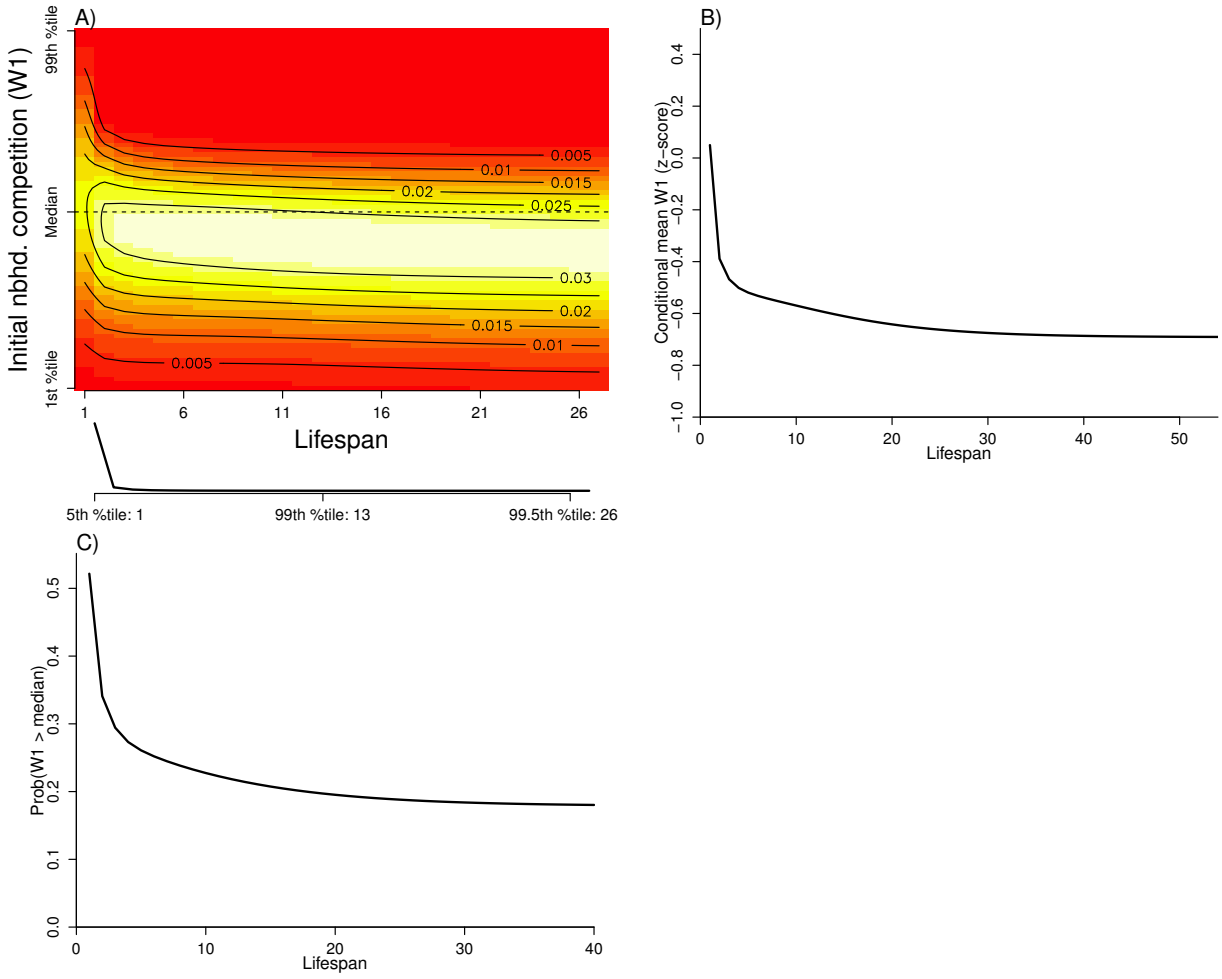

Figure 7: [Figure 7 caption here.]

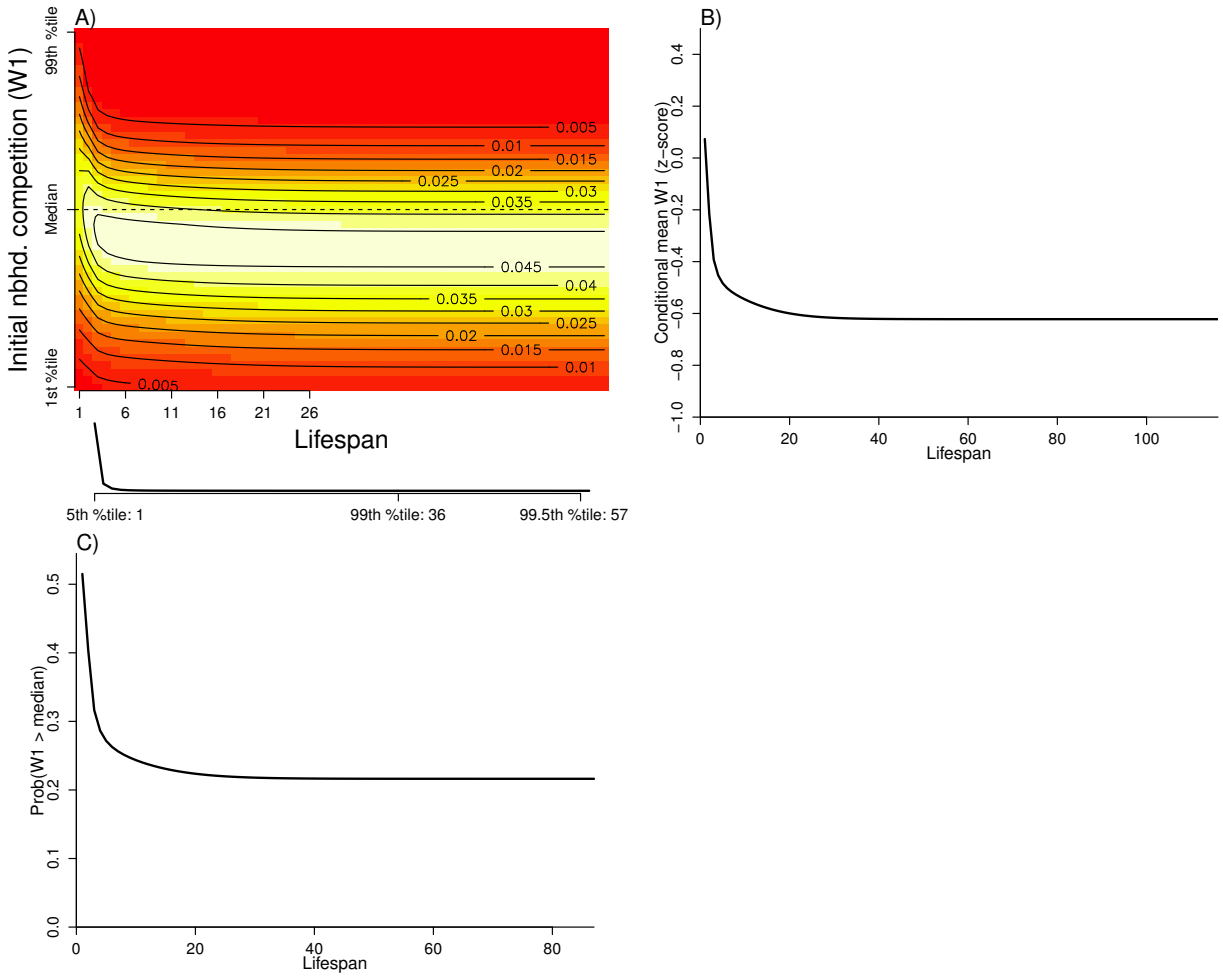

Figure 8: [Figure 8 caption here.]

Online Appendix

A Analysis for the two-stage models

First we note some general small-variance approximations. Let f be any smooth function of x. Taylor-expand

$$f(x) = f(\bar{x}) + f'(\bar{x})\sigma Z + \frac{1}{2}f''(\bar{x})\sigma^2 Z^2 + O(\sigma^3). \tag{A1}$$

Taking expectations of both sides of (A1),

$$\mathbb{E}\, f(x) \approx f(\bar{x}) + \frac{1}{2}f''(\bar{x})\sigma^2. \tag{A2}$$

Taking the variance of both sides of (A1),

$$\begin{aligned} Var\, f(x) &\approx Var(f'(\bar{x})\sigma Z) + Var(\frac{1}{2}f''(\bar{x})\sigma^2 Z^2) + 2\, Cov(f'(\bar{x})\sigma Z, \frac{1}{2}f''(\bar{x})\sigma^2 Z^2) \\ &= f'(\bar{x})^2\sigma^2 + O(\sigma^4) + \sigma^3 f'(\bar{x})f''(\bar{x})\, Cov(Z, Z^2) \\ &\approx f'(\bar{x})^2\sigma^2. \end{aligned} \tag{A3}$$

Note that if Z has a symmetric distribution $Cov(Z, Z^2) = Cov(-Z, (-Z)^2) = -\,Cov(Z, Z^2)$, so $Cov(Z, Z^2) = 0$ and the variance approximation will have $O(\sigma^4)$ error. Similarly,

$$Cov(f(x), g(x)) \approx f'(\bar{x})g'(\bar{x})\sigma^2. \tag{A4}$$

For any model, we can consider $V_{\mathbb{T}}$ and $V_{\mathbb{L}}$ to be functions of σ and calculate $V_{\mathbb{T}}(\sigma)/(V_{\mathbb{L}}(\sigma) + V_{\mathbb{T}}(\sigma))$ to leading order in σ. Recall that $V_{\mathbb{T}}$ is the variance with respect to x of expected LRS as a function of x. Equation (A3) therefore tells us that $V_{\mathbb{T}}(\sigma) = O(\sigma^2)$. Meanwhile, $V_{\mathbb{L}}$ is the expectation with respect to x, of the variance in LRS given x. Equation (A2) therefore tells us that $V_{\mathbb{L}}(\sigma) = V_{\mathbb{L}}(0) + O(\sigma^2)$. Therefore

$$\frac{V_{\mathbb{T}}(\sigma)}{V_{\mathbb{L}}(\sigma) + V_{\mathbb{T}}(\sigma)} = \frac{V_{\mathbb{T}}(\sigma)}{V_{\mathbb{L}}(0)} + O(\sigma^4). \tag{A5}$$

Another useful simplification is that (for example) $\overline{F}$ and $F(\bar{x})$ differ by $O(\sigma^2)$, so to leading order it is often the case that one of them can replace the other.

Iteroparous model

In this model, conditional on the values of the demographic traits, lifetime reproductive success is $R = BZ$ where $B \sim$ Bernoulli(s_J) and Z is the sum of D random variables with mean F and variance $Var(C)$. We therefore have $\mathbb{E}[Z] = \mathbb{E}[D]F = LF$, and thus the expected LRS given trait x is

$$\mathbb{E}(R|x) = s_J(x)L(x)F(x). \tag{A6}$$

We also have

$$\begin{aligned} Var(R) &= \mathbb{E}(B)^2\, Var(Z) + Var(B)\, \mathbb{E}(Z)^2 + Var(B)\, Var(Z) \\ &= s_J^2\, Var(Z) + s_J(1-s_J)(\mathbb{E}(Z)^2 + Var(Z)) \\ &= s_J\, Var(Z) + s_J(1-s_J)\, \mathbb{E}(Z)^2. \end{aligned} \tag{A7}$$

The standard formula for the sum of N *iid* random variables C_i, where N is random and independent of the C_i is

$$Var(\sum_{i=1}^{N} C_i) = \mathbb{E}[N]\, Var(C) + (\mathbb{E}[C]^2)\, Var(N), \tag{A8}$$

and thus $Var(Z) = L\, Var(C) + F^2\, Var(D)$. Combining this with eq. A7, we arrive at

$$Var(R|x) = s_J(x)\left(L(x)\, Var(C|x) + F^2(x)\, Var(D|x)\right) + s_J(x)(1-s_J(x))L^2(x)F^2(x). \tag{A9}$$

We want an expression for $V_{\mathbb{T}}(\sigma)/V_{\mathbb{L}}(0)$ to order σ^2. Because $V_{\mathbb{T}}(\sigma)$ is $O(\sigma^2)$ we only need the value of $V_{\mathbb{L}}(0)$ to $O(1)$, so we can use equation (A9) with $\overline{F}$ in place of $F(\bar{x})$, and so on, getting

$$V_{\mathbb{L}}(0) = Var(LRS|x=\bar{x}) \approx \bar{s}_J\left(\overline{L}\, Var(C|\bar{x}) + \overline{F}^2\, Var(D|\bar{x})\right) + \bar{s}_J(1-\bar{s}_J)\overline{L}^2\overline{F}^2. \tag{A10}$$

$V_{\mathbb{T}}$ is the variance with respect to x of $E(R|x) = s_J(x)L(x)F(x)$. From (A3), to leading order this is σ^2 times the squared derivative with respect to x of $s_J LF$,

$$V_{\mathbb{T}}(\sigma) \approx (s_J'\overline{L}\,\overline{F} + \bar{s}_J L'\overline{F} + \bar{s}_J\overline{L}F')^2\sigma^2. \tag{A11}$$

using the fact that to leading order $\overline{F} = F(\bar{x})$, and so on. The meaning of the $V_{\mathbb{T}}$ approximation is clearer if we express it in terms of trait variances and covariances. Assuming that small variation in x produces small variation in F, L, and s_J, we can Taylor expand in these variables to get

$$\begin{aligned} V_{\mathbb{T}}(\sigma) &= Var(s_J LF) \\ &\approx (\bar{s}_J\overline{L}\,\overline{F})^2\Big[CV^2(s_J) + CV^2(L) + CV^2(F) + 2CC^2(s_J,L) + 2CC^2(s_J,F) + 2CC^2(L,F)\Big], \end{aligned} \tag{A12}$$

where $CV(X)$ is the coefficient of variation of X ($CV^2(X) = Var(X)/\bar{X}^2$) and $CC(X,Y)$ is the coefficient of covariation of X and Y ($CC^2(X,Y) = Cov(X,Y)/(\bar{X}\bar{Y})$). We therefore have

$$\begin{aligned} \frac{V_{\mathbb{T}}}{V_{\mathbb{T}}+V_{\mathbb{L}}} \approx \frac{V_{\mathbb{T}}(\sigma)}{V_{\mathbb{L}}(0)} \approx \frac{\bar{s}_J^2}{\bar{s}_J\left(\dfrac{CV^2(C|\overline{F})}{\overline{L}} + CV^2(D|\overline{L})\right) + \bar{s}_J(1-\bar{s}_J)} \Big[CV^2(s_J) + CV^2(L) + CV^2(F) \\ + 2CC^2(s_J,L) + 2CC^2(s_J,F) + 2CC^2(L,F)\Big], \end{aligned} \tag{A13}$$

with the term in square brackets being of order σ^2.

Semelparous model

An individual's lifetime reproductive success is $R = B_j B_b C$, where $B_j \sim \text{Bernoulli}(s_J)$ and $B_b \sim \text{Bernoulli}(b/(d+b))$. The expected lifetime reproductive success given trait x is the probability of surviving to adulthood ($s_J(x)$) times the probability of reproducing ($b(x)/(d(x)+b(x))$), times the expected clutch size ($F(x)$):

$$\mathbb{E}(R|x) = \frac{s_J(x)b(x)}{d(x)+b(x)}F(x). \tag{A14}$$

Again, $V_{\mathbb{T}}$ is the variance with respect to x of $\mathbb{E}(R|x)$. As before, we assume that variation in x causes small variation in one or more of the model parameters. Taylor expanding to second order in all of the parameters and taking the expectation to leading order, as in eq. A3, this is

$$\left(\frac{\partial}{\partial s_J}\frac{\bar{s}_J\bar{b}\bar{F}}{\bar{d}+\bar{b}}\right)^2 Var(s_J) + \left(\frac{\partial}{\partial b}\frac{\bar{s}_J\bar{b}\bar{F}}{\bar{d}+\bar{b}}\right)^2 Var(b) + \ldots + 2\left(\frac{\partial}{\partial s_J}\frac{\bar{s}_J\bar{b}\bar{F}}{\bar{d}+\bar{b}}\right)\left(\frac{\partial}{\partial b}\frac{\bar{s}_J\bar{b}\bar{F}}{\bar{d}+\bar{b}}\right) Cov(s_J, b) + \ldots. \tag{A15}$$

Taking the derivatives produces

$$\begin{aligned} V_{\mathbb{T}}(\sigma) \approx{}& \left(\frac{\bar{s}_J\bar{b}}{\bar{d}+\bar{b}}\right)^2 Var(F) + \left(\frac{\bar{b}\,\bar{F}}{\bar{d}+\bar{b}}\right)^2 Var(s_J) + \frac{\bar{s}_J^2\bar{F}^2\bar{d}^2}{(\bar{d}+\bar{b})^4}\,Var(b) + \frac{\bar{s}_J^2\bar{F}^2\bar{b}^2}{(\bar{d}+\bar{b})^4}\,Var(d) \\ &+ 2\frac{\bar{s}_J\bar{b}^2\bar{F}}{(\bar{d}+\bar{b})^2}\,Cov(s_j, F) + 2\frac{\bar{s}_J\bar{b}\,\bar{F}^2 d}{(\bar{d}+\bar{b})^3}\,Cov(s_j, b) - 2\frac{\bar{s}_J\bar{b}^2\bar{F}^2}{(\bar{d}+\bar{b})^3}\,Cov(s_j, d) \\ &+ 2\frac{\bar{s}_J^2\bar{b}\,\bar{F}\,\bar{d}}{(\bar{d}+\bar{b})^3}\,Cov(F, b) - 2\frac{\bar{s}_J^2\bar{b}^2\bar{F}}{(\bar{d}+\bar{b})^3}\,Cov(F, d) - 2\frac{\bar{s}_J^2\bar{b}\,\bar{F}^2 d}{(\bar{d}+\bar{b})^4}\,Cov(b, d). \end{aligned} \tag{A16}$$

Factoring out $(\bar{s}_J\bar{b}/(\bar{d}+\bar{b}))^2$, the expected LRS when all traits take their average value, we get

$$\begin{aligned} V_{\mathbb{T}}(\sigma) \approx{}& \left(\frac{\bar{s}_J\bar{b}\,\bar{F}}{\bar{d}+\bar{b}}\right)^2 \left(CV_F^2 + CV_{s_j}^2 + \frac{\bar{d}^2}{(\bar{d}+\bar{b})^2}(CV_b^2 + CV_d^2)\right. \\ &+ \frac{2}{\bar{s}_J\bar{F}}CC^2(s_j, F) + 2\frac{\bar{d}}{\bar{s}_J\bar{b}(\bar{b}+\bar{d})}CC^2(s_j, b) - \frac{2}{\bar{s}_J(\bar{b}+\bar{d})}CC^2(s_j, d) \\ &\left.+ 2\frac{\bar{d}}{\bar{b}\,\bar{F}(\bar{b}+\bar{d})}CC^2(F, b) - \frac{2}{\bar{F}(\bar{b}+\bar{d})}CC^2(F, d) - 2\frac{\bar{d}}{\bar{b}(\bar{b}+\bar{d})^2}CC^2(b, d)\right). \end{aligned} \tag{A17}$$

The reproductive variance is

$$\begin{aligned} Var(R|x) &= (\mathbb{E}\,C)^2\,Var(B_jB_b) + Var(C)\,\mathbb{E}(B_jB_b)^2 + Var(C)\,Var(B_jB_b) \\ &= F^2\,Var(B_jB_b) + Var(C)\left(\frac{s_J b}{d+b}\right)^2 + Var(C)\,Var(B_jB_b), \end{aligned} \tag{A18}$$

where

$$\begin{aligned} Var(B_jB_b) &= \mathbb{E}(B_j)^2\, Var(B_b) + Var(B_j)\, \mathbb{E}(B_b)^2 + Var(B_j)\, Var(B_b) \\ &= s_J^2 \frac{bd}{(d+b)^2} + s_J(1-s_J)\left(\frac{b}{d+b}\right)^2 + s_J(1-s_J)\frac{bd}{(d+b)^2} \\ &= s_J \frac{bd}{(d+b)^2} + s_J(1-s_J)\left(\frac{b}{d+b}\right)^2 x, \end{aligned} \tag{A19}$$

where s_J, b, d, and F are all functions of x. The luck contribution is then, to first order,

$$\begin{aligned} V_{\mathbb{L}}(\sigma^2 = 0) &= Var(LRS|x = \overline{x}) \\ &= \overline{F}^2 \left[\frac{\overline{s}_J \overline{bd}}{(\overline{d}+\overline{b})^2} + \overline{s}_J(1-\overline{s}_J)\left(\frac{\overline{b}}{\overline{d}+\overline{b}}\right)^2\right] + \left(\frac{\overline{b}\overline{s}_J}{\overline{d}+\overline{b}}\right)^2 Var(C|\overline{F}) \\ &\quad + \left(\frac{\overline{s}_J \overline{bd}}{(\overline{d}+\overline{b})^2} + \frac{\overline{b}^2 \overline{s}_J(1-\overline{s}_J)}{(\overline{d}+\overline{b})^2}\right) Var(C|\overline{F}) \\ &= \left(\frac{\overline{s}_J \overline{b}\,\overline{F}}{\overline{d}+\overline{b}}\right)^2 \left[\frac{\overline{d}}{\overline{s}_J\overline{b}} + \frac{1-\overline{s}_J}{\overline{s}_J} + \frac{Var(C|\overline{F})}{\overline{F}^2}\left(1 + \frac{\overline{d}}{\overline{s}_J\overline{b}} + \frac{1-\overline{s}_J}{\overline{s}_J}\right)\right]. \end{aligned} \tag{A20}$$

The relative contribution of trait to variance in lifetime reproductive success is thus

$$\begin{aligned} \frac{V_{\mathbb{T}}}{V_{\mathbb{T}} + V_{\mathbb{L}}} \approx & \frac{CV_F^2 + CV_{s_J}^2 + \frac{\overline{d}^2}{(\overline{d}+\overline{b})^2}(CV_b^2 + CV_d^2)}{\left(\frac{\overline{d}}{\overline{s}_J\overline{b}} + \frac{1-\overline{s}_J}{\overline{s}_J}\right)\left(1 + CV^2(C|\overline{F})\right) + CV^2(C|\overline{F})} \\ & + \frac{\frac{2}{\overline{s}_J\overline{F}} CC^2(s_j, F) + 2\frac{\overline{d}}{\overline{s}_J\overline{b}(\overline{b}+\overline{d})} CC^2(s_j, b) - \frac{2}{\overline{s}_J(\overline{b}+\overline{d})} CC^2(s_j, d)}{\left(\frac{\overline{d}}{\overline{s}_J\overline{b}} + \frac{1-\overline{s}_J}{\overline{s}_J}\right)\left(1 + CV^2(C|\overline{F})\right) + CV^2(C|\overline{F})} \\ & + \frac{2\frac{\overline{d}}{\overline{b}\,\overline{F}(\overline{b}+\overline{d})} CC^2(F, b) - \frac{2}{\overline{F}(\overline{b}+\overline{d})} CC^2(F, d) - 2\frac{\overline{d}}{\overline{b}(\overline{b}+\overline{d})^2} CC^2(b, d)}{\left(\frac{\overline{d}}{\overline{s}_J\overline{b}} + \frac{1-\overline{s}_J}{\overline{s}_J}\right)\left(1 + CV^2(C|\overline{F})\right) + CV^2(C|\overline{F})}. \end{aligned} \tag{A21}$$

B Size-structured model with individual quality variation

Here we present the detailed assumptions, numerical methods, and results for the "prototype" size-structured IPM. The model's basic structure is typical of many in the current literature, but each demographic rate model has an additional term so that outcomes are affected by a "quality" variable q that is assigned at birth and remains constant over the lifetime. We think of size (denoted x) as a log-transformed size measure because linear demographic models, such as the ones we specify below, have often been found to be appropriate for log-transformed size (log mass, log basal area, etc.).[6] In the model, size x typically ranges between -1 to 3; individuals are born with size near 0 (with mean size possibly depending on q), and the growth model results in an asymptotic "adult" size near 2 (with the exact value possibly depending on q).

For calculating the importance of luck, $V_{\mathbb{L}}/V_{\mathbb{T}}$, we will assume a population in which q has a Gaussian distribution with mean 0 and variance 1. Model parameters with CV in their name then represent a coefficient of variation, which is always chosen small enough that negative values of demographic rates are rare enough.

The model's main demographic rate functions are plotted in fig. B1 for two sets of parameter values (Table B1) that give contrasting life histories: relatively short expected lifespan with high per-capita annual fecundity (row 1) vs. longer life with lower annual fecundity (row 2).

- Survival probability is a logistic regression in size, $\text{logit}s(x) = s_1(x - s_0) + 2s_1 CV_s q$. The coefficient on q implies that CV_s is the approximate (to leading order in q) coefficient of variation in survival (as a function of q) at the size s_0 where $s = 0.5$ for an average-quality individual ($q = 0$). A unavoidable consequence of the logistic regression model is that between-individual variation in survival is small when average survival is near zero or 1.

- Fecundity: for our calculations we need to specify the size- and quality-dependent mean and variance of per-capita annual offspring production, but not the specific distribution. We assume that the mean is the maximum of 0 and $b_F(x - x_c)(1 + qCV_F)$. Then CV_F is the CV (across individuals) of size-dependent expected per-capita fecundity. The variance is assumed to be an allometric function of the size-dependent mean, Variance = $A(\text{Mean})^b$, $A, b > 0$).

- Initial size of new offspring is Gaussian with mean $qCV_{x,0}$, and variance $\sigma^2_{x,0}$. If x is a log-transformed size measure, then $CV_{x,0}$ is approximately the CV of size on the arithmetic scale when q has variance 1.

- Growth is modeled by linear regression. Size at time $t + 1$, conditional on being size x at time t, is Gaussian with mean $b_G x + (1 - b_G)\bar{x}$ and variance σ^2_G, where $0 < b_G < 1$ and $\bar{x} = 1 + qCV_{\bar{x}}$. Here b_G is the slope of the regression line, and the intercept term is written in terms of the point $\bar{x}$ at which the regression line intersects the 1:1 line. That intersection point is the asymptotic size to which individuals would converge, in the absence of any random variability in growth. Because q has variance 1 by assumption, $CV_{\bar{x}}$ is approximately the between-individual CV of asymptotic size on the arithmetic scale.

[6] For this model only, we follow the notation for size-quality models in (Ellner et al., 2016, Chapter 6) in which x is size and q is quality, to reduce the rate of errors when adapting code and formulas from that source. This far outweighs the disadvantage of having x mean one thing in the main text and something different here.

Depending on the CV parameters, individual quality q can affect any or all of: initial size, expected size-dependent growth rate, size-dependent survival, and size-dependent fecundity. Figures B2 and B3 show the resulting age-dependent vital rates across the range of individual quality q at the two sets of baseline parameters in Table B1.

A complication in variance partitioning for this model is that the trait q can affect both initial size and the subsequent dynamics of size. The basic partitioning is equation (1), which for this model is

$$Var(R) = \underbrace{\mathbb{E}_q(Var(R|q))}_{\text{luck}} + \underbrace{Var_q(\mathbb{E}(R|q))}_{\text{trait variation}}. \tag{B1}$$

Similar to the perennial plant models, we need to expand each term to account for the fact that R depends on initial size x_0 which can be correlated with q. For trait variation,

$$\mathbb{E}(R|q) = \int \mathbb{E}(R|x_0, q)c_0(x_0|q)dx_0 \tag{B2}$$

where $c_0(x_0|q)$ is the conditional distribution of x_0 given quality q. $\mathbb{E}(R|x_0, q)$ can be computed from a size-only model where all individuals have quality q, in the usual way. Let P_q be the survival/growth kernel for quality q, N_q the corresponding fundamental operator $(I - P_q)^{-1}$, and $\beta_q(x)$ the expected per-capita fecundity as a function of size x; then $\mathbb{E}(R|x_0, q) = \beta_q N_q$ and so

$$\mathbb{E}(R|q) = \beta_q N_q c_0(x|q). \tag{B3}$$

For the luck term, the methods of (Ellner et al., 2016, Section 3.2) can be used to compute $Var(R|x_0, q)$ as a function of x_0 for any q using a size-only IPM for individuals with constant quality q. Then

$$Var(R|q) = \mathbb{E}_{x_0}(Var(R|x_0, q)) + Var_{x_0}(E(R|x_0, q)) \tag{B4}$$

where the mean and variance above are computed with respect to the conditional distribution of x_0 given quality q.

In a midpoint rule implementation of the IPM, the two last equations will produce vectors of $\mathbb{E}(R|q)$ and $Var(R|q)$ values at the quality meshpoints, which can be used to compute the terms in (B1) for any assumed distribution of q.

Results for the size-structured model

For each baseline parameter set, the LRS variance decomposition and other life-cycle properties were calculated for 250 random parameter sets generated by independent Gaussian perturbations to the log of each parameter, with mean 0 and standard deviation 0.2; this gives lognormal parameter variation with a CV of approximately 20%. Figs. B4 and B5 show that lifespan is (as we would expect by now) a key attribute in the variance partitioning. Mean and standard deviation of lifespan are very tightly correlated (panel A); the dashed line is a regression line through the origin of that plot.[7] Both $V_{\mathbb{T}}$ and $V_{\mathbb{L}}$ tend to increase with longer expected lifespan (panels B and C), in such a way that $V_{\mathbb{T}}/(V_{\mathbb{T}} + V_{\mathbb{L}})$ is fairly small and appears to approach an asymptote with increasing mean lifespan, at which trait-dependent variation is $\approx$ 35% (fig. B4) or 25% (fig. B5)of the total.

[7]Lifespan is defined to be the number of censuses at which an individual is alive. This implies that the minimum possible lifespan is 1, so lifespan-1 is the number of years of non-guaranteed survival.

Sensitivity analysis of $V_{\mathbb{T}}/(V_{\mathbb{T}}+V_{\mathbb{L}})$ with respect to model parameters (Table B2) also highlights the importance of lifespan variability. For both baseline parameter sets, the demographic parameters with highest sensitivity were those determining the mean (and therefore the variance) of lifespan (s_0 and s_1, the parameters of the logistic regression of survival on size, and the growth regression slope b_G, which determines how quickly individuals escape the high mortality rate of small individuals). Similarly, the effect of quality on annual survival (CV_s) had higher sensitivity than the other CV parameters; for the second parameter set individual variation in size at birth (CV_{x0}) and asymptotic size ($CV_{\bar{x}}$) were also important, because high-quality individuals reach the minimum size for reproduction several years sooner than low-quality individuals (fig. B3B).

The contribution of trait variation in figs. B4D and B5D depends on the amount of between-individual fitness variation at the baseline parameter sets (see figs. B2D and B3D). As with the two-stage models, empirical estimates of selection strength (Kingsolver et al., 2012) are a useful benchmark. In both parameter sets, the trait-dependent variation in annual fecundity and the trait-dependent variation in survival (specified by the values of CV_F and CV_s) are both above the estimated median value of the selection gradient on individual traits ($|\beta|$, Kingsolver et al., 2012, Table S2). The resulting selection gradients $|\beta|$ for (survival$\times$fecundity) are ≈ 0.45 in both parameter sets, roughly twice the estimated mode of $|\beta|$ values for total fitness measures in natural populations where directional selection was detected (Kingsolver et al., 2012, Table S2). Our baseline parameter sets thus produce above-average but not exceptionally high levels of between-individual fitness variation, relative to natural populations.

The resulting values of $V_{\mathbb{T}}/(V_{\mathbb{T}}+V_{\mathbb{L}})$ (figs. B4 and B5) thus confirm the conclusion from our two-stage models: for realistic levels of among-individual variation in traits affecting fitness, trait-dependent variance in LRS can sometimes be a nontrivial component of the total variance, but it will typically be dominated by variance due to luck.

Table B1: Baseline parameter vectors for the size-quality model.

s_0	s_1	b_G	σ_{x1}	σ_{x0}	b_F	x_c	A	b	CV_s	CV_F	$CV_{\bar{x}}$	CV_{x0}
0.50	1.00	0.60	0.20	0.10	0.75	1.00	1.00	1.00	0.25	0.25	0.05	0.10
-2.00	0.50	0.70	0.20	0.10	0.50	1.50	0.50	1.00	0.25	0.20	0.10	0.20

Note: s_0 is the size at which survival = 0.5 (which can be negative, because we assume a log-transformed size measure); s_1 is the slope of logit survival as a function of size; b_G is the slope of the linear regression of size at $t+1$ on size at t and σ_{x1} is the conditional standard deviation of size at $t+1$; σ^2_{x0} is the standard deviation of initial size; b_F is the slope of the fecundity function above x_c, the minimum size at which reproduction occurs; A and b are parameters of the variance-mean relationship for annual offspring production; the CV parameters determine the coefficient of variation in demographic rates, as explained in the text.

Table B2: Parameter sensitivity analysis for the two baseline parameter vectors in Table B1.

Parameter	Set 1	Set 2
s_0	-0.13	-0.16
s_1	0.45	0.57
b_G	-0.77	-0.75
σ_{x1}	-0.01	0.04
σ_{x0}	0.00	0.00
b_F	0.05	0.01
x_c	-0.05	-0.07
A	0.02	-0.05
b	-0.03	0.05
CV_s	0.41	0.22
CV_F	0.05	0.06
$CV_{\bar{x}}$	0.09	0.15
CV_{x0}	0.03	0.13

Note: the tabulated values are standardized regression coefficients calculated by the `src` function in the `sensitivity` R package. Because the randomly perturbed parameter sets were generated with standard deviation $\approx$ 20% of the baseline value, the standardized coefficients are proportional to elasticities (specifically, they give the estimated absolute change in the response for a 20% change in the parameter). The coefficients were calculated by the function `src` in the `sensitivity` R package (`CRAN.R-project.org/package=sensitivity`). Calculations are performed in `SizeQualityElasticityAnalysis.R`

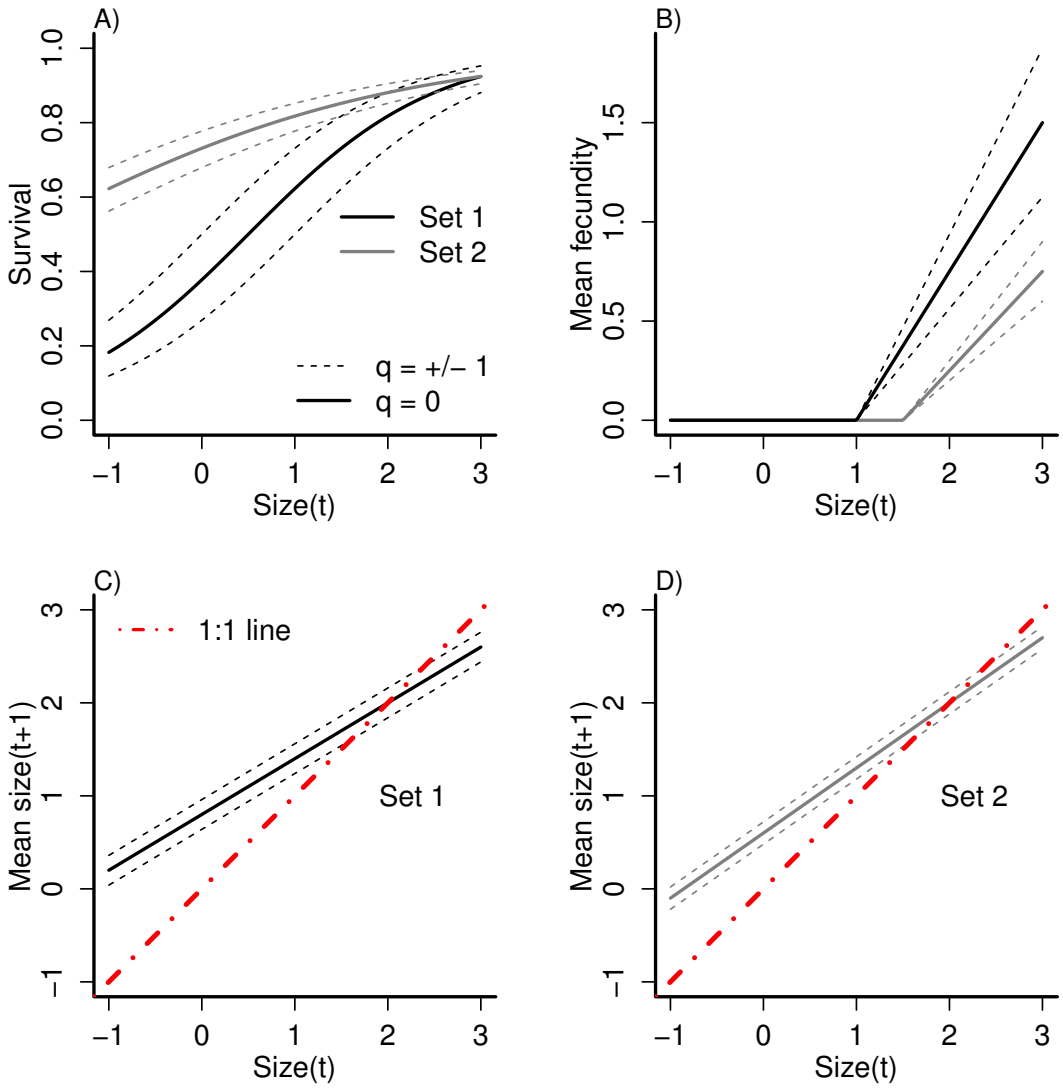

Figure B1: [Figure B1 caption here.]

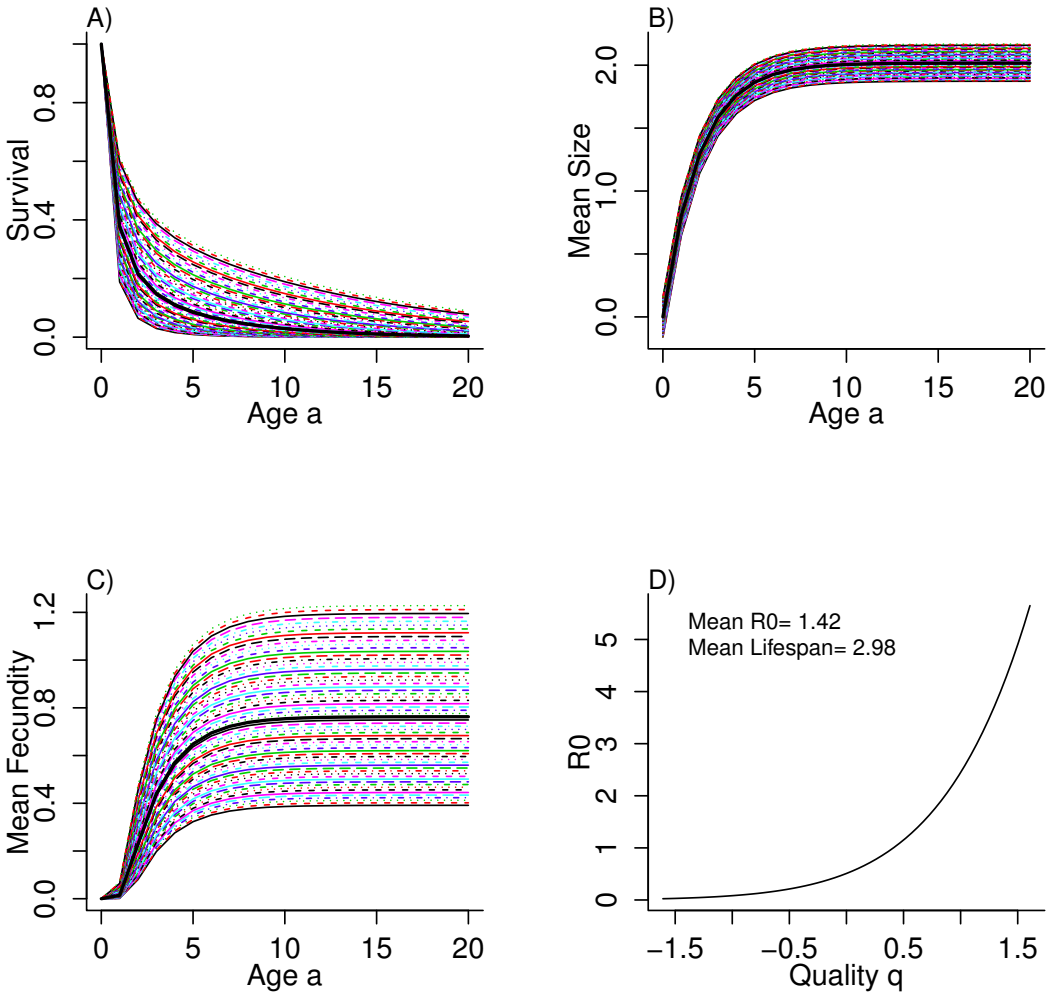

Figure B2: [Figure B2 caption here.]

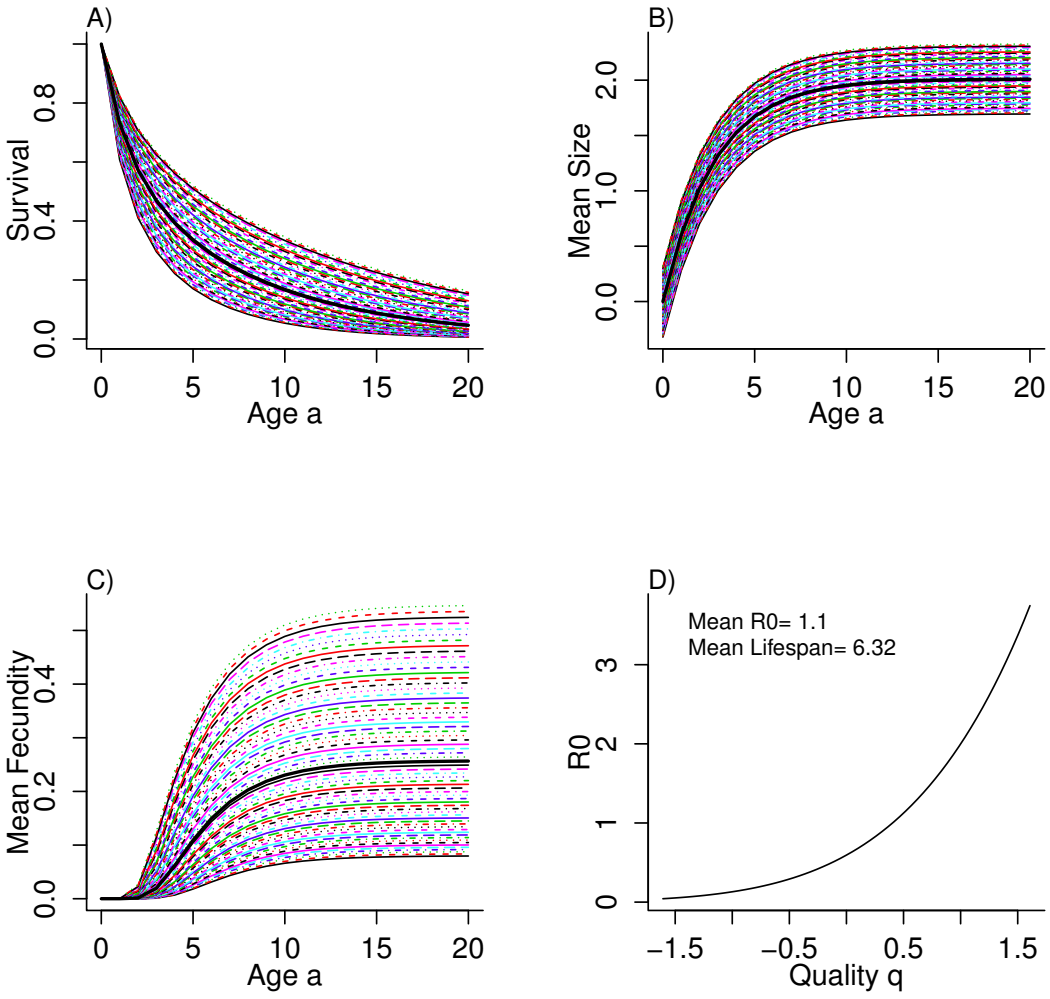

Figure B3: [Figure B3 caption here.]

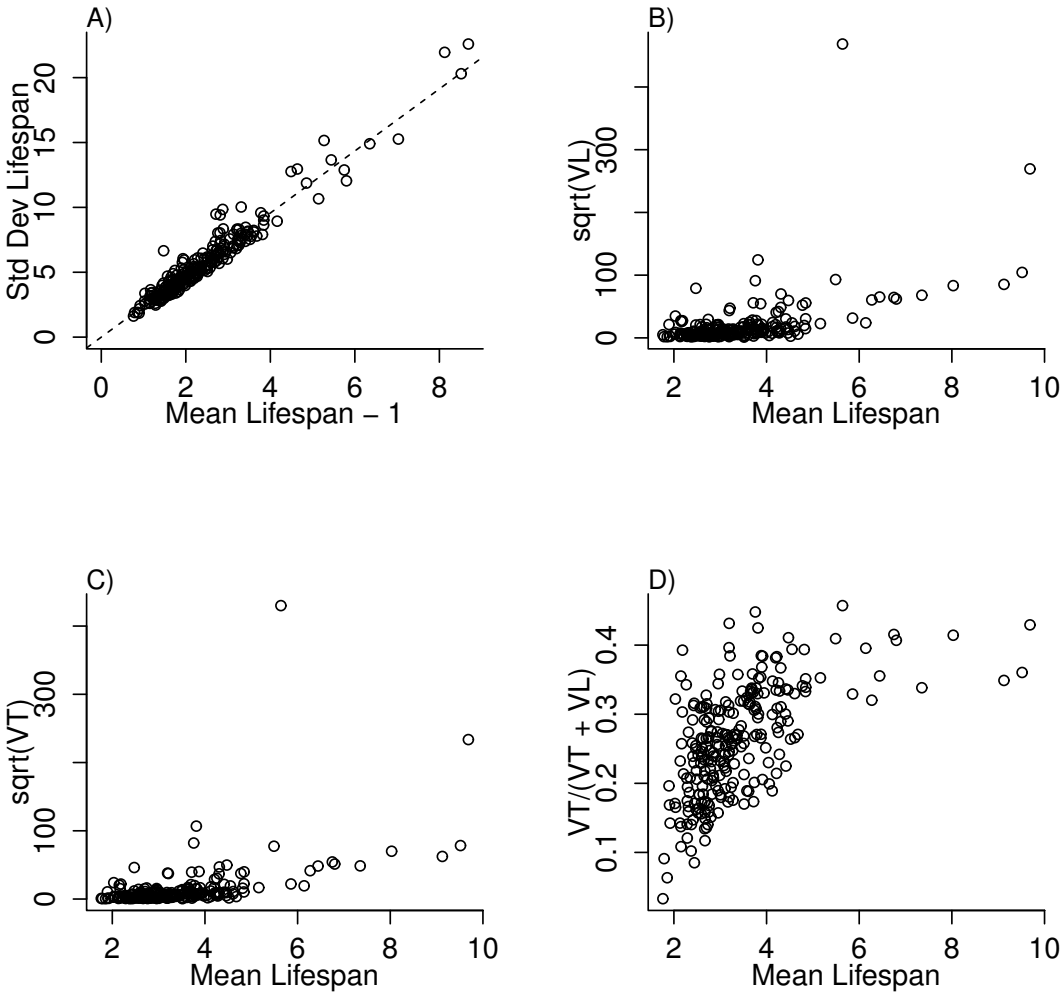

Figure B4: [Figure B4 caption here.]

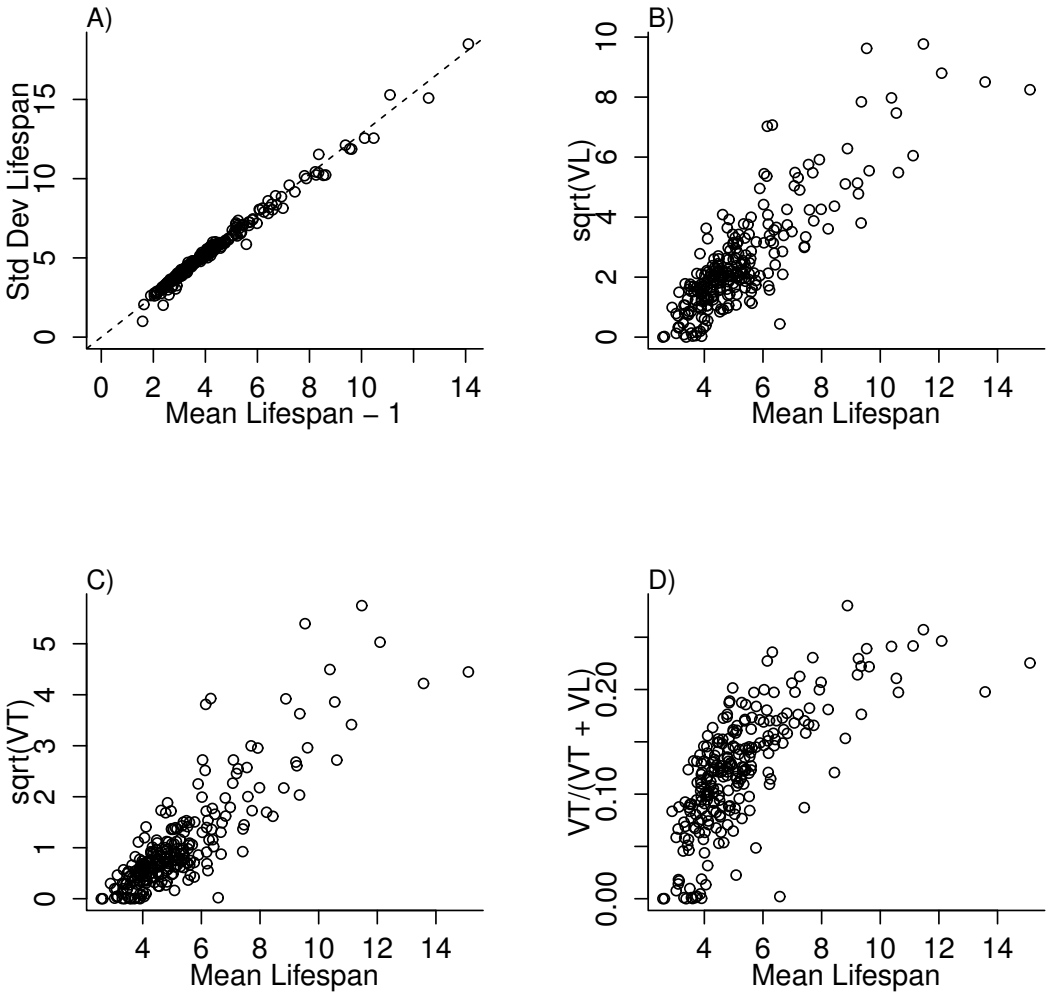

Figure B5: [Figure B5 caption here.]

C Perennial plant single-species IPMs

Here we develop relatively simple integral projection models (IPM) for the four most common species in the Idaho sagebrush steppe community studied by Adler et al. (2010), in which individuals are cross-classified by size and by competitive pressure, W. These are used in the main text with the individual trait being the competitive pressure at age 1, W_1. Like a genotype, this trait is assigned at birth and has long-lasting effects, because an individual's competitive neighborhood changes gradually over time.

Structurally these models are a standard size$\times$quality IPM, except that seedlings are modeled separately because they differ from older plants in two ways: seedlings have higher mortality (all else being equal), and the subsequent size of surviving individuals is affected by W in older individuals but not in seedlings. Scripts for the calculations are in the folder `SingleSppIpm` in the online SI.

The four dominant species are the shrub, *Artemisia tripartita* (ARTR), and the C3 perennial bunchgrasses *Pseudoroegneria spicata* (PSSP), *Hesperostipa comata* (HECO), and *Poa secunda* (POSE). These species accounted for over 70% of basal cover (grasses) and 60% of canopy cover (shrubs and forbs) during the period of data collection, 1926-1957. See (Adler et al., 2010) for details on the study area and methods of data collection and data processing. Models with all of the components needed for our analysis are developed only for ARTR and PSSP, for reasons explained below, but we consider the other species as well to provide additional support for the model structure.

Previous studies of this system (Adler et al., 2010; Chu and Adler, 2015) have found that between-species competition among the dominant species is much weaker than within-species competition, in many cases not significantly different from zero. Removal experiments (Adler et al. *in review*) have confirmed the resulting prediction that removals of competing species would have little effect on the remaining species. For our purposes here, including between-species competition would mean that survival and growth would have slightly different W covariates, because the coefficients determining the between-species impacts are different for survival and growth. The model would then be much more cumbersome to work with, for little gain in accuracy. We therefore consider models with only within-species competition, using the nonparametric competition kernels fitted by Teller et al. (2016). In an initial analysis that included between-species competition (not described here), we found that the estimated within- and between-species components of total competition pressure were nearly independent (correlation coefficient $|r| < 0.15$ for both survival and growth in PSSP, $|r| \leq 0.05$ for survival and growth in the other three species). Between-species competition can therefore be viewed as a small amount of random "noise" added to the much larger effect of within-species competition.

Seedlings are only partially identified in the original quadrat maps, so for all analyses here, likely seedlings are identified by size and age. However, individuals recorded as `age=1` in a quadrat that was not observed the previous year are actually of unknown age. Such individuals, if they are small, might be seedlings or they might be older individuals that shrank to a seedling-like size. So for all analyses of seedlings only, or of older individuals only, we removed from the data set all such "doubtful" individuals: small (size ≤ 0.25 cm^2) and recorded as `age=1` in a quadrat that was not observed the previous year. With doubtful individuals removed, any remaining individual who is small (size ≤ 0.25 cm^2) and recorded as `age=1` are classified as seedlings, and all others are classified as older. This assumes that any individuals larger than

0.25 cm^2 is older, regardless of their recorded age. The function to trim out doubtful individuals and identify likely seedlings is in `TrimQuadrats.R`.

Seedlings are different

To test whether seedlings are demographically different, we fitted survival models that included a factor variable flagging likely seedlings. A significantly nonzero coefficient for this variable implies that seedlings behave differently, all else being equal. Specifically, we fitted the model

```
gam(survives ~ logarea + W + Group + seedling + seedling:Group
               + s(year,bs="re") + s(year,by=logarea,bs="re")
               + s(year,by=W,bs="re"), family=binomial)
```

where W is within-species competition. The model includes random year effects on the intercept, the slope in size, and slope in W.

For all four species, the coefficient on `seedling` was significantly negative, with $p < 0.01$. Several of the of the `seedling:Group` interaction coefficients were also significant, though most were not. Script file: `CompareSeedlings.R`.

Seedling growth also needs a separate model. Close to 100% of seedlings and likely seedlings are recorded as "too small to measure" and assigned area 0.25cm^2, so the subsequent size of survivors at age 2 is necessarily independent of initial size. In addition, we will see below that survivor size at age 2 is also independent of W at age 1, whereas the growth of older individuals is affected by W. Putting these facts together, a reasonable model for seedlings is that

1. They are born with a random value of local crowding W (drawn from the empirical distribution of W for seedlings), which determines their probability of surviving to age 2.

2. Those who survive are assigned a random size, drawn from the empirical distribution of sizes for seedlings that survive to age 2.

3. W is modeled as a Markov Chain (see below). W at age 1 therefore determines the distribution of W at age 2.

The fact that seedlings are different is a re-discovery of what Chu and Adler (2014) found: in many species age matters, as well as size. Chu and Adler (2014) fitted models with `1/age` as a covariate, and possibly also an interaction between size and `1/age`. In most cases, AIC comparisons favored age-dependence in addition to size-dependence.

For the Idaho species, addition of age to a model with size- and year-dependent survival adds $< 2\%$ to the amount of deviance explained (with or without an age:size interaction). A model with covariates `seedling` and `seedling:logarea` picks up much of the additional deviance explained (38% in ARTR, 59-75% in the others (this is done in script `Fit_Survival_Seedlings.R`). To avoid a three-way classification by age, size, and W, we simplify the age structure to seedlings vs. older plants.

Modeling seedling survival

Survival of seedlings was modeled with logistic regression,

	Seedlings		Age 2 and up		
Species	a_0	b_W	a_0	b_z	b_W
ARTR	-1.76	-1.86	0.75	0.57	-1.55
HECO	-0.24	-1.67	1.86	1.26	-2.08
POSE	-0.33	-2.20	1.70	1.01	-3.76
PSSP	-1.05	-1.26	1.98	1.43	-2.22

Table C1: Parameters for logistic regression models of survival. For seedlings, logit $s = a_0 + b_W W$. For older plants, logit $s = a_0 + b_z z + b_W W$. Source files: `Fit_Survival_Seedlings.R`, `Fit_Survival_Older.R`

```
gam(survives ~ W + s(Group,bs="re") + s(year,bs="re") + s(year,by=W,bs="re"),
               family=binomial)
```

This model includes a Group random effect, random year effects on the intercept and slope with respect to W. Recall that seedling size is not included in the model, because nearly all seedlings were recorded as too small to measure. For a minimal-luck model, we drop the random variation in slope and intercept and use the fitted mean intercept and slope (Table C1). Nonlinear responses to W were tested by fitting the same model with an `s(W)` term; there was no evidence of a deviation from the logistic regression.

A test of the seedling survival model is how well it predicts the distribution of W values at age 1 for seedlings that survive to age 2 (Figures C1 – C4). Indeed, getting this right is the main thing that the survival model needs to do in the context of our analyses. For ARTR the mortality at higher W values may be slightly over-estimated, though it is hard to be sure because the number of surviving recruits is so small; otherwise there is a very good match between the observed and predicted initial W distributions for seedlings that survive to age 2.

Modeling older plant survival

For non-seedlings we adopted the logistic regression model used in previous studies of this system, with random year effects on the intercept, slope with respect to size, and competition coefficient (slope with respect to W).

```
gam(survives ~ logarea + W + s(Group,bs="re") + s(year,bs="re")
          + s(year,bs="re",by=logarea) + s(year,bs="re",by=W), family=binomial)
```

The estimated coefficients for the minimal-luck model (omitting year effects) are in Table C1.

As with seedlings, we compared the logistic regression model to a nonlinear model with a spline response to W. Again, there was no evidence against the linear response to W, and the predictions of the linear and nonlinear models were almost perfectly correlated ($r > 0.99$ for all species).

We also compared the logistic regression model to one with a nonlinear response to initial size (i.e., an `s(logarea)` term in the linear predictor). For ARTR there was evidence of nonlinearity ($\Delta AIC \approx 13$ in favor of the spline model) but the nonlinearity was weak and the predictions of the linear and nonlinear models were very similar (correlation $r = 0.98$); for the other species, the predictions from the linear and nonlinear models were nearly identical ($r > 0.995$). We therefore again retained the linear model.

Species	f	d	σ
ARTR	0.65	1.61	1.31
HECO	0.76	-0.20	0.80
POSE	0.45	-0.07	0.70
PSSP	0.58	-0.16	0.76

Table C2: Parameters of the Gaussian mixture model for the size at age 2 of surviving seedlings, $f \times N(\log(0.25), 0.2^2) + (1-f) \times N(d, \sigma^2)$. Source file `Fit_Growth_Seedlings.R`

Modeling seedling growth

The data sets record the same size for almost all seedlings, so the only question is whether W affects the subsequent size of surviving seedlings. The answer appears to be "no". For survivors, there is no correlation between W at age 1 and size at age 2 (script `Fit_Growth_Seedlings.R`, using the `Kendall` library to compute Kendall's rank-correlation coefficient τ between W at age 1 and size at age 2:

```
ARTR tau = -0.0632, 2-sided pvalue =0.65623
HECO tau = 0.0478,  2-sided pvalue =0.35902
POSE tau = -0.0272, 2-sided pvalue =0.55299
PSSP tau = 0.027,   2-sided pvalue =0.61293
```

Similarly, fitting seedling growth with

```
gam(logarea.t1 ~ W + s(year,bs="re"))
```

the coefficient of W was not significant for any species ($p > 0.35$).

These results about seedling survival and growth lead to a model where seedlings are classified only by W, which determines their survival probability. Their size at age 2 is a random draw independent of W, and their W at age 2 is a random draw from the Markov Chain for $W(t)$ described below, conditional on their initial W.

A majority of age-2 individuals are still recorded as "too small to measure" (area = 0.25cm^2). For the IPM we need a smoothed version of the size distribution at age 2. A mixture of two Gaussians, representing "too small" and other individuals, gives a reasonably good fit (fig. C5). The "too small" component has mean= $\log(0.25)$, standard deviation= 0.2, by fiat. The distribution parameters are the fraction in the left peak, and the mean and standard deviation of the second peak. These were estimated by maximum likelihood (source file `Fit_Growth_Seedlings.R`) and the estimates are in Table C2.

Modeling older plant growth

As a first exploratory step, we used `gam` fits to check for nonlinearity in the responses to initial size and to W. The linear and nonlinear models produced nearly identical predictions (see fig. C6). For ARTR the linear model slightly under-predicts the growth of the largest and smallest individuals, and in the other species the linear and nonlinear models make nearly identical predictions.

We therefore adopted the linear model used in previous studies of this system, a linear mixed-effects model with size-dependent variance. However, we modeled growth variability using a

Student-t distribution with estimated df parameter. The limit $df \to \infty$ gives a Gaussian distribution; finite df gives fatter tails. As it turns out, small values of df are estimated for all species.

Fitting was done in a Bayesian framework, because this is the only available option for a model with random year-effects and t-distributed growth variability. We used JAGS (via the `rjags` library). The full model (with random Group effects, and random year effects on the intercept, z-slope, and competition coefficient) mixed very slowly. Group effects proved to be the cause. With very vague priors on group effects and on the overall intercept, MCMC chains could drift to regions where the variance parameter for Group effects is very large, and the mean Group effect is far from zero but compensated by an equal but opposite intercept coefficient. Once a chain gets there, getting back to the actual region of highest likelihood is difficult because it requires a simultaneous jump (in the right directions) by all Group means and the intercept coefficient.

This problem was removed by putting an informative prior on Group effects. In the `lmer` fits, estimated Group effects were mostly non-significant, and always small (mostly < 0.2 in magnitude and all < 0.5). The prior we used for Group effects was Gaussian with standard deviation 0.5. With 3 chains, 5000 burn-in iterations and 25000 sampled iterations with 10-fold thinning, this gave sufficiently fast mixing (Gelman-Rubin scale reduction factor of 1.05 or lower for all parameters) in all species but PSSP. For PSSP the multivariate scale reduction factor was 1.2, so we re-ran with 50000 iterations and 20-fold thinning, which brought the factor down to 1.13.

The "minimal-luck" model ignores Group effects and year-to-year variation in growth parameters:

$$\begin{aligned} \mathbb{E}[z_{t+1}] &= a_0 + a_1 z_t + b_W W \\ z_{t+1} - \mathbb{E}[z_{t+1}] &\sim t(\tau(z_t), df) \\ \tau(z) &= \tau_0 e^{cz} \end{aligned} \tag{C1}$$

As parameterized in JAGS, the Student-t distribution with k degrees of freedom and precision τ and has density

$$t(x|\tau,k) = \frac{\Gamma\left(\frac{k+1}{2}\right)}{\Gamma\left(\frac{k}{2}\right)} \sqrt{\frac{\tau}{k\pi}} \left(1 + \frac{\tau x^2}{k}\right)^{-(k+1)/2}. \tag{C2}$$

Unfortunately, it is not the case that τ is the inverse of the variance, as it is for the Gaussian distribution in JAGS.

Table C3 below gives the parameter estimates for all species (mean of the MCMC samples after burn-in). The a_0 coefficient is the sum of the estimated intercept and the estimated Group effects; this is equivalent to centering the Group effects at zero, so that a_0 represents a "typical" Group. The fitted model also includes random year effects on all a and b coefficients. The "minimal luck" model ignores these components of luck, except that the growth variability in the "minimal luck" model is the variability that remains after Group and year effects are accounted for in the fitted model.

In Table C3, b_W is the estimate of the mean coefficient on W, and $\langle b_W(t) \rangle$ is the average of the year-specific estimates. The former is a rather complicated object. Year-specific b_W is specified as a Gaussian (whose mean d_b and precision τ_b are parameters to be estimated), but that distribution is truncated onto an interval $(-L, 0)$ so its actual mean is not equal to d_b. The values for b_W in the

	a_0	a_1	b_W	$< b_W(t) >$	τ	c	df
ARTR	0.4930	0.9231	-0.0722	-0.0697	1.2196	0.4227	2.2393
HECO	0.2403	0.8969	-0.2898	-0.2779	3.5924	0.1413	3.2284
POSE	0.3868	0.7195	-0.5622	-0.5363	1.4732	0.0861	10.0740
PSSP	0.2405	0.8921	-0.3300	-0.3383	1.8594	0.2529	4.8425

Table C3: Estimated parameters for "minimal luck" non-seedling growth model with only intraspecific competition, fitted with JAGS. Source files `Fit_Growth_JAGS.R`,`jags_growth.txt`, and `JAGS_tables_v3.R`.

Tables were calculated by computing the actual mean of the truncated Gaussian distribution for each (d_b, τ_b) pair in the 3 MCMC chains that were run, and averaging those values. The adjacent column $\langle b_W(t) \rangle$ is the average of the ≈ 20 year-specific estimates of b_W; its similarity to the b_W estimate is reassuring.

Recruitment

Previous analyses of these data have modeled recruitment at the quadrat level, rather than the level of individual plants, because the census data do not let us identify which parent plant produced which recruits. But our analyses here require a model for individual fecundity, so we take a different approach. Although previous analyses have identified year-to-year variability and density-dependence as important factors in recruitment, we omit both of those to construct a simple "minimal luck" model in which seed production is a deterministic function of individual size, and the only random variation in recruitment ("luck" in our analyses) is random survival (or not) of seeds to become recruits the next year. A model that omits most "luck" in recruitment is adequate for our purposes here, because even when we do this, the conclusion (as reported in the main text) is that effects of trait (i.e., initial W) variation is overwhelmed by luck.

Measurements of number of inflorescences per plant in PSSP (P. Adler, *unpublished data*) suggest that inflorescence number is proportional to the square root of plant area ($e^{z/2}$ for z=log area). We assume that expected seed production is proportional to inflorescence number. If seed production is large, with a small fraction of seeds surviving to become measured recruits, the number of recruits (conditional on the number of seeds produced) should have a Poisson distribution. We therefore assumed that recruit production by a size-z individual is Poisson with mean $m(z) = Ce^{z/2}$. The constant C cannot be estimated from our data. For all calculations with the models, we therefore chose C to make the population stable ($\lambda = 1$ in the overall IPM).

Modeling changes in W

Our analyses also require a model for how the "trait" W changes over time. For two of the species (ARTR, PSSP) it was possible to construct a simple first-order model consistent with the data; for the other two, the dynamics are more complicated and may require a higher-order model (i.e., $W(t)$ depends on $W(t-2)$ and possibly early values, not just on $W(t-1)$). A higher-order model for W ups the dimension of the resulting IPM, which is then computationally intractable. We therefore consider only ARTR and PSSP here and in the main text.

The models for W dynamics were fitted to the estimated W values for all individuals who were observed at a time t and a subsequent time $t+1$, regardless of age (known or unknown). We

Species	a_W	b_W	a_σ	b_σ	df	W_0
ARTR	-0.0734	0.9545	0.5380	0.0217	2.5663	0.0025
PSSP	-0.3125	0.8624	0.4563	0.0427	4.5233	0.0025

Table C4: Parameters for AR(1) models of log-transformed W fitted with `gamlss`. Source file: `ModelingW.R`

.

have seen that some seedlings land in locations with exceptionally high W, but these individuals are not included in the data on W dynamics because they don't survive to be censused a second time.

The distributions of W are strongly right-skewed, but after log-transformation to reduce the skew, the dynamics are fitted well by a first-order autoregressive process with Student-t residuals and nonconstant variance. The models were fitted by linear regression of $\log(W_0 + W(t+1))$ on $\log(W_0 + W(t))$ using the `gamlss` package; $W_0 = 0.0025$ (corresponding to 1% of a new recruit) was added to avoid zero values. Diagnostic plots for the fitted models (as provided by `plot.gamlss`) suggested that the models fitted well (specifically, the actual distribution of scaled residuals was close to a t distribution with the fitted df). Fitted parameters (in Table C4) are the intercept a_W and slope b_W for the conditional mean, intercept a_σ and slope b_σ for the standard deviation as a linear function of $\log(W_0 + W(t+1))$, and the degrees of freedom df for the t distribution.

Constructing the IPM iteration matrix

Functions that implement the demographic models and construct the IPM iteration matrices are in the script `drivers/Rpartition/empirical/IdahoIPMFunctions.R`.

Individuals age 2 and up are described by a standard size-quality IPM, with W as the individual quality variable. Using `mx` mesh points for size, and `mW` mesh points for W, the two-dimensional state vector has length `mx*mW` in the sequence produced by `expand.grid` applied to the size and W mesh points: all sizes with the first value of W, then all sizes with the second value of W, and so on. Survival and growth of individuals age 2 and up is therefore represented by an iteration matrix P_2 with `mx*mW` rows and the same number of columns. For numerical accuracy, the IPM is implemented with $\log(W_0 + W)$ rather than W as the state variable, and all vital rate functions in the IPM back-transform to W values before applying the fitted demographic models.

To add seedlings to the model, we prepend to the state vector `mW` mesh points representing seedlings. The iteration matrix for the full IPM including seedlings is then structured like a Lefkovitch matrix with two age classes, age$=1$ and age>1,

$$K = \begin{pmatrix} 0 & F_2 \\ P_1 & P_2 \end{pmatrix}. \tag{C3}$$

The upper-left 0 matrix is `mW` by `mW`. This block of K would represent transitions within the seedling class, but in our model there are none because age-2 individuals are treated as (small) adults.

Submatrix P_1 is survival from seedling to older. It has `mx*mW` rows and `mW` columns. The j^{th} column is the seedling survival at the j^{th} meshpoint for W, multiplied by the state distribution

conditional on survival. The state distribution conditional on survival is the product of the size distribution at age 2 (which is the same for all columns) with the distribution of $W(t+1)$ conditional on the starting value of W.

Submatrix F_2 is fecundity of older individuals, proportional to square-root of area and independent of W (for lack of data). It has `mW` rows (seedlings at all W values) and `mx*mW` columns. Columns $j = 1$ to `mx` are the W distribution of seedlings, multiplied by the fecundity at the j^{th} size meshpoint. The remaining `mx* (mW-1)` columns of F_2 are `mW-1` copies of this block of columns, for the remaining W values of older plants.

The constant of proportionality for fecundity multiplies all elements in F_2. We choose its value so that the iteration matrix has $R_0 = 1$ and therefore a dominant eigenvalue of 1. To find the value, we first compute F_2 with the constant set equal to 1. The resulting initial R_0 is the dominant eigenvalue of the seedlings-to-seedlings next-generation operator $F_2(I - P_2)^{-1}P_1$. (This is also what one gets from the standard next generation operator $R = F(I - P)^{-1}$ with $K = P + F$, using the fact that the eigenvalues of a block-triangular matrix are the eigenvalues of the diagonal blocks.) We then re-set the constant of proportionality to $1/R_0$ (equivalently, divide F_2 by the initial R_0). This results an F_2 such that $R_0 = 1$, as desired.

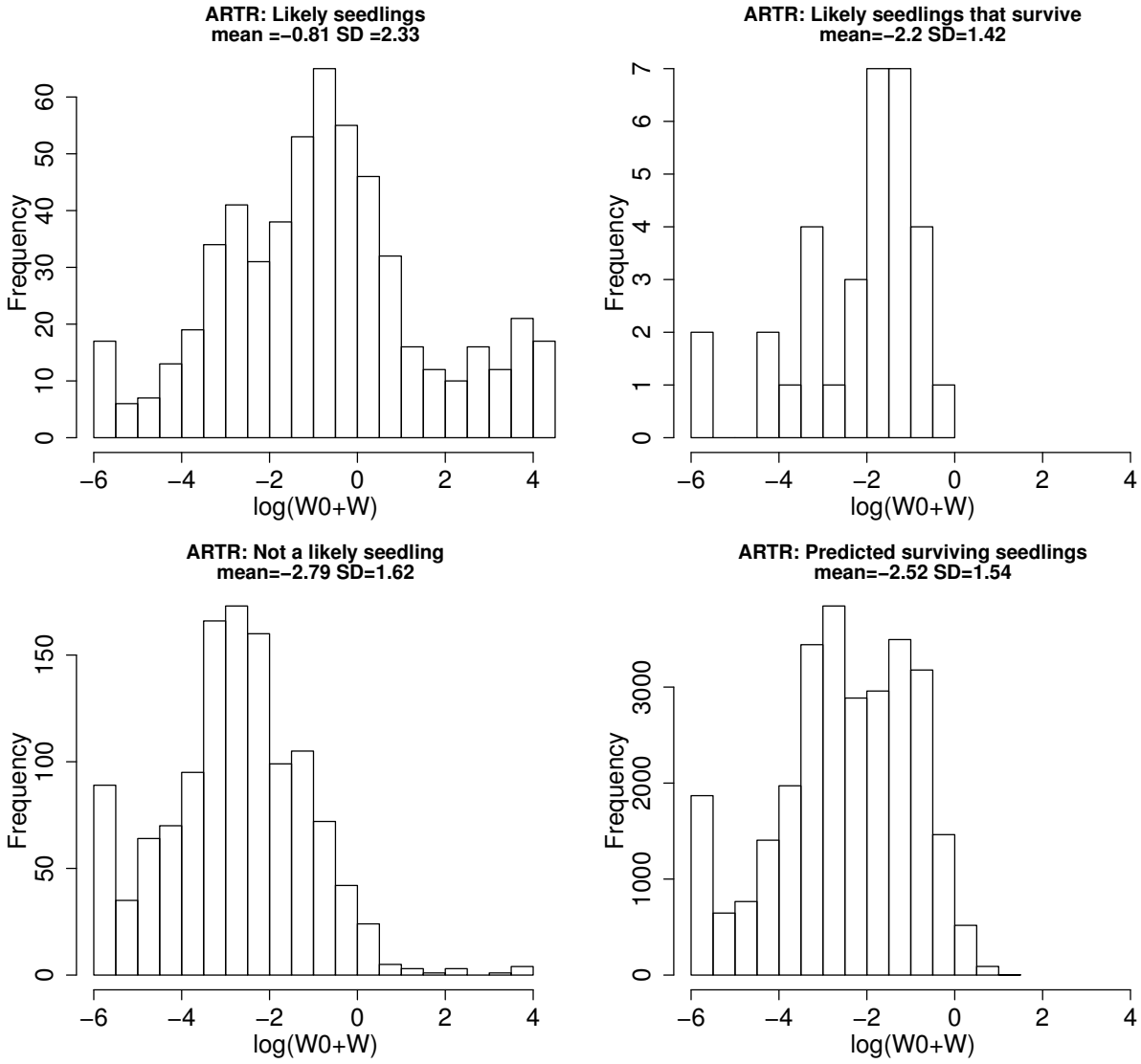

Figure C1: [Figure C1 caption here.]

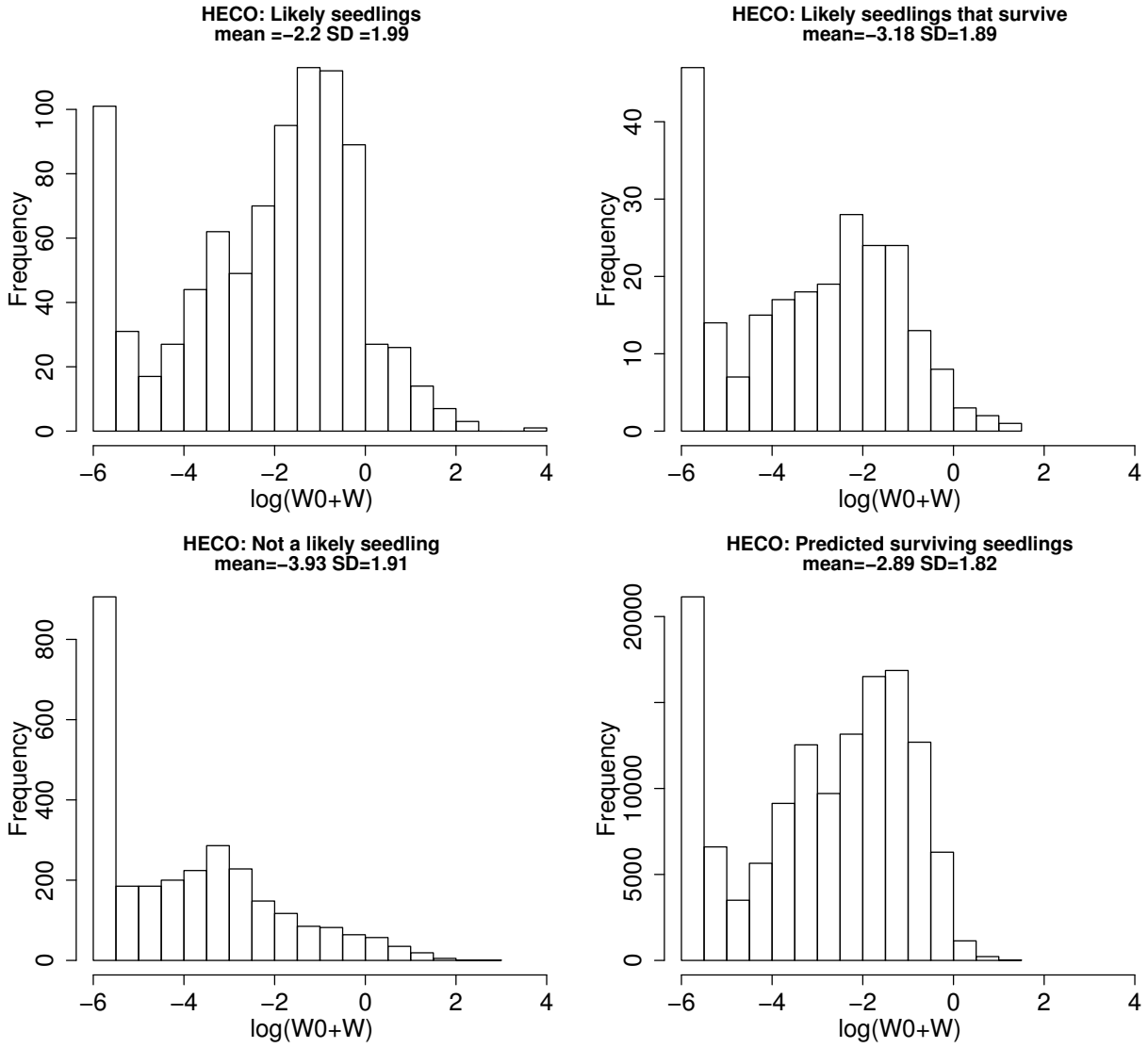

Figure C2: [Figure C2 caption here.]

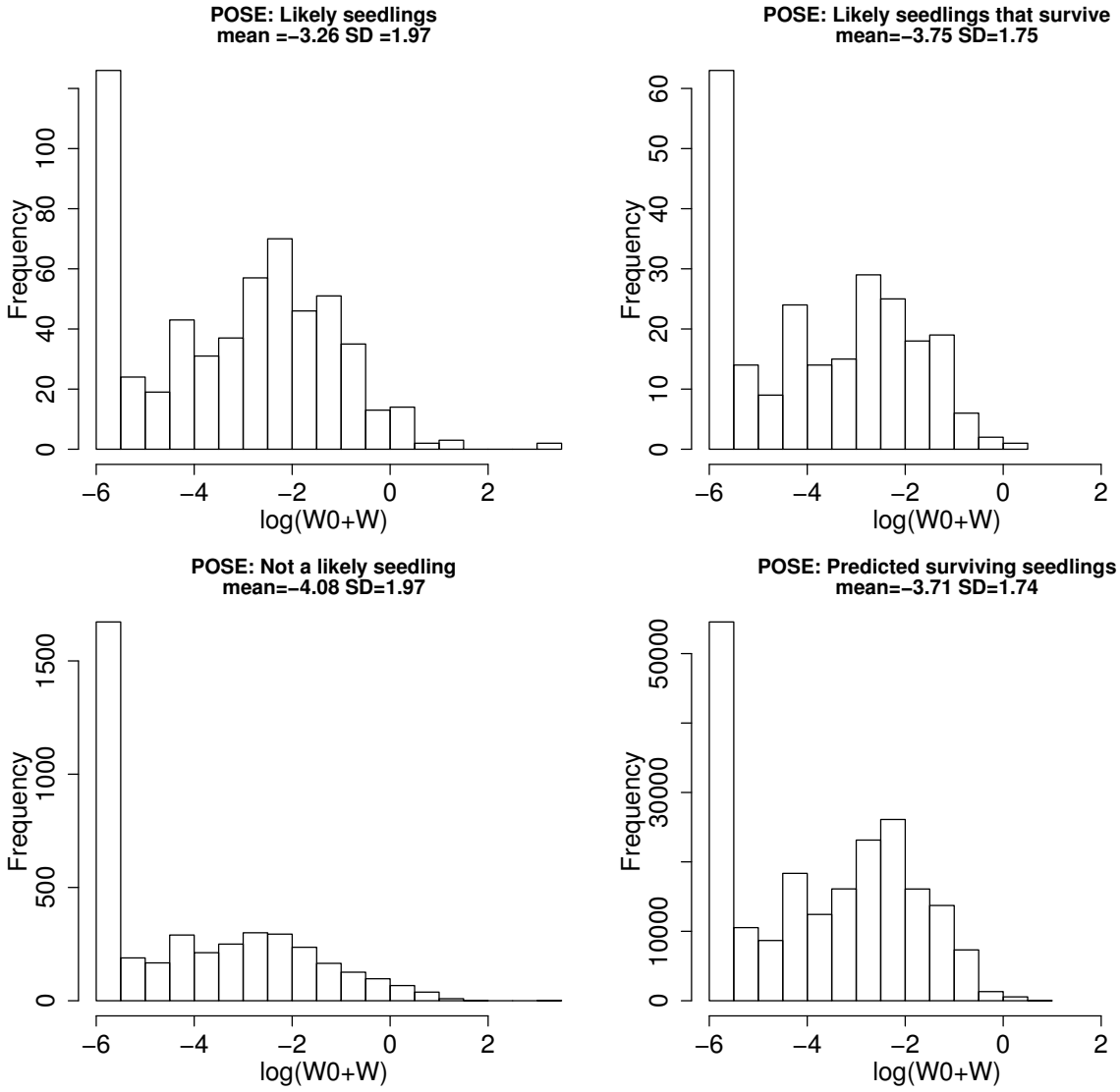

Figure C3: [Figure C3 caption here.]

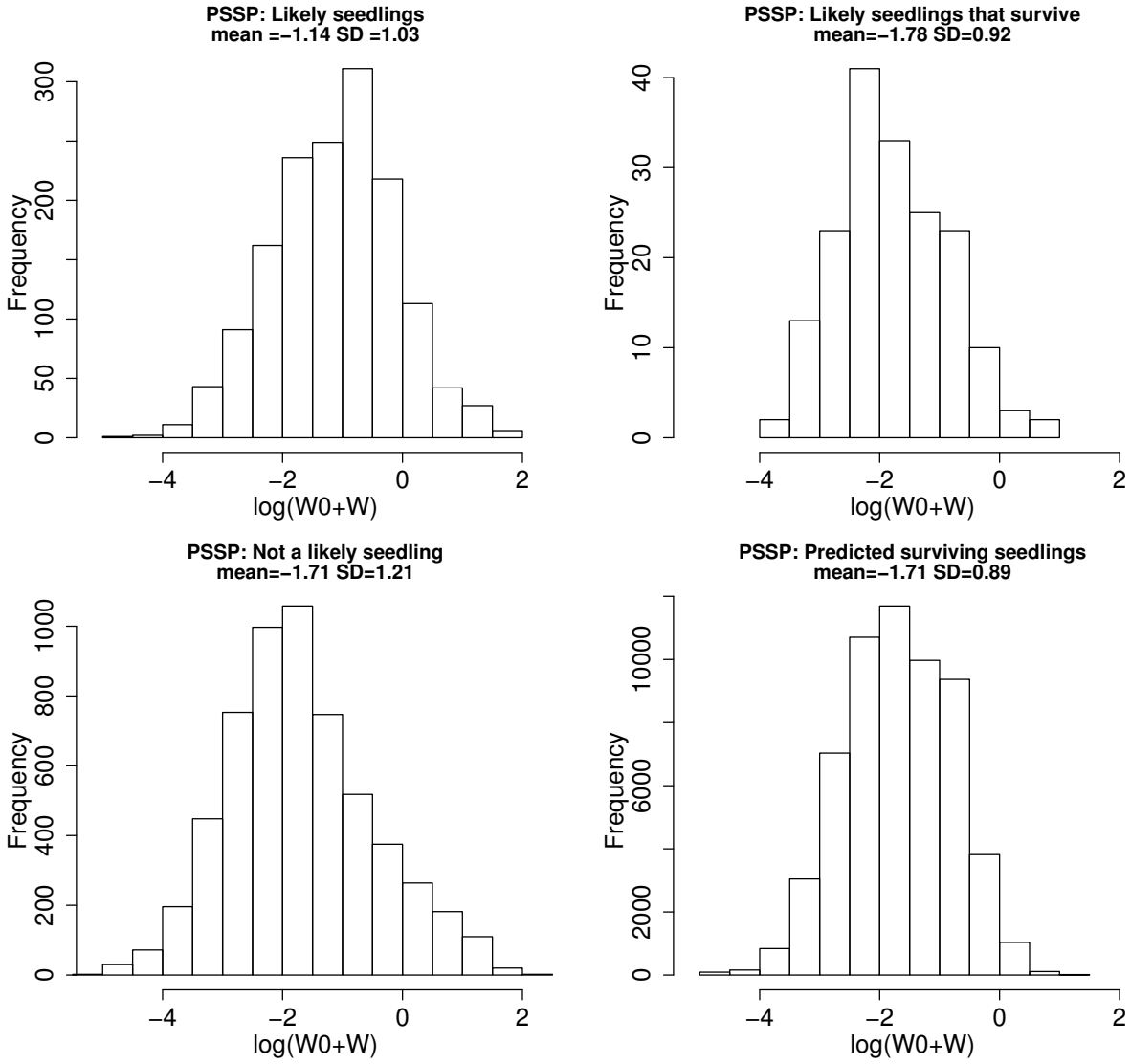

Figure C4: [Figure C4 caption here.]

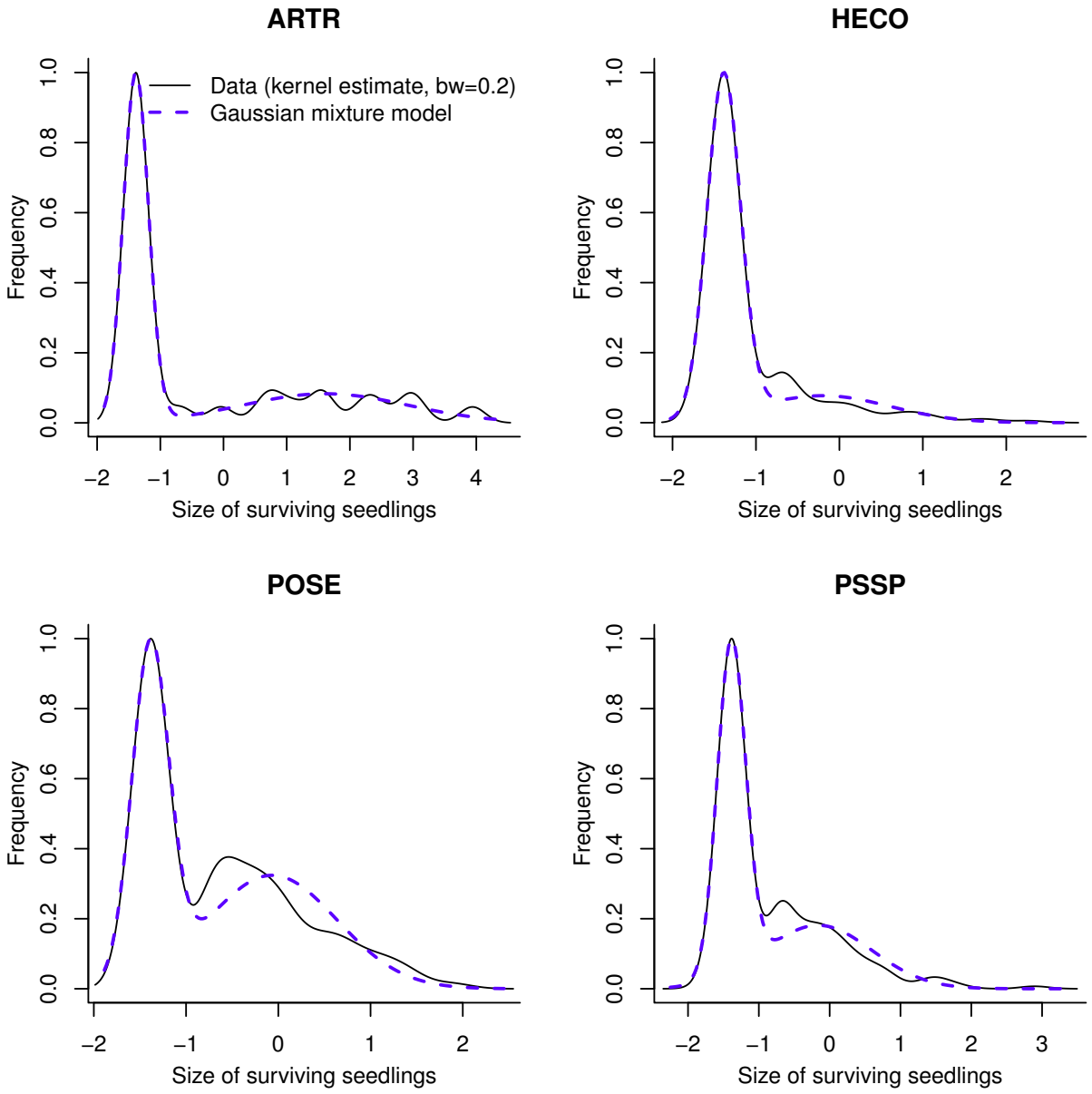

Figure C5: [Figure C5 caption here.]

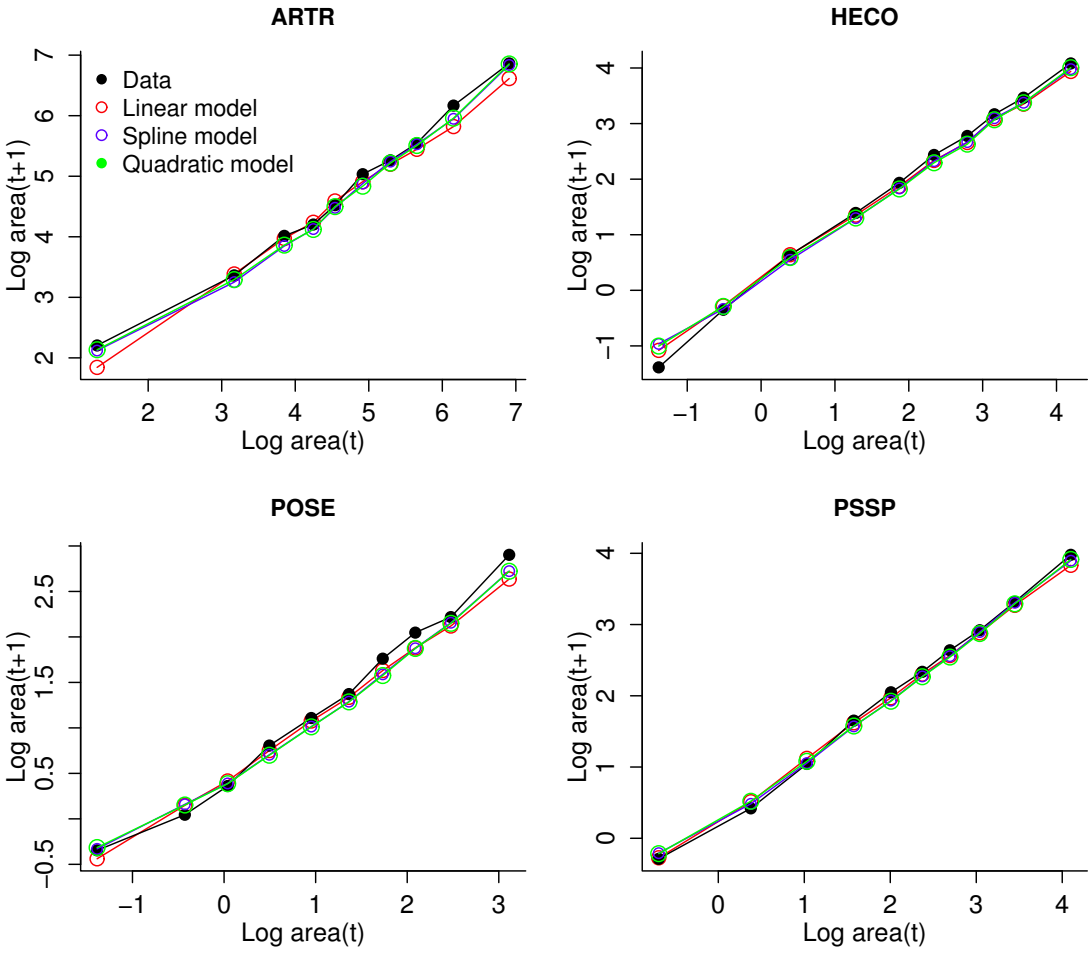

Figure C6: [Figure C6 caption here.]

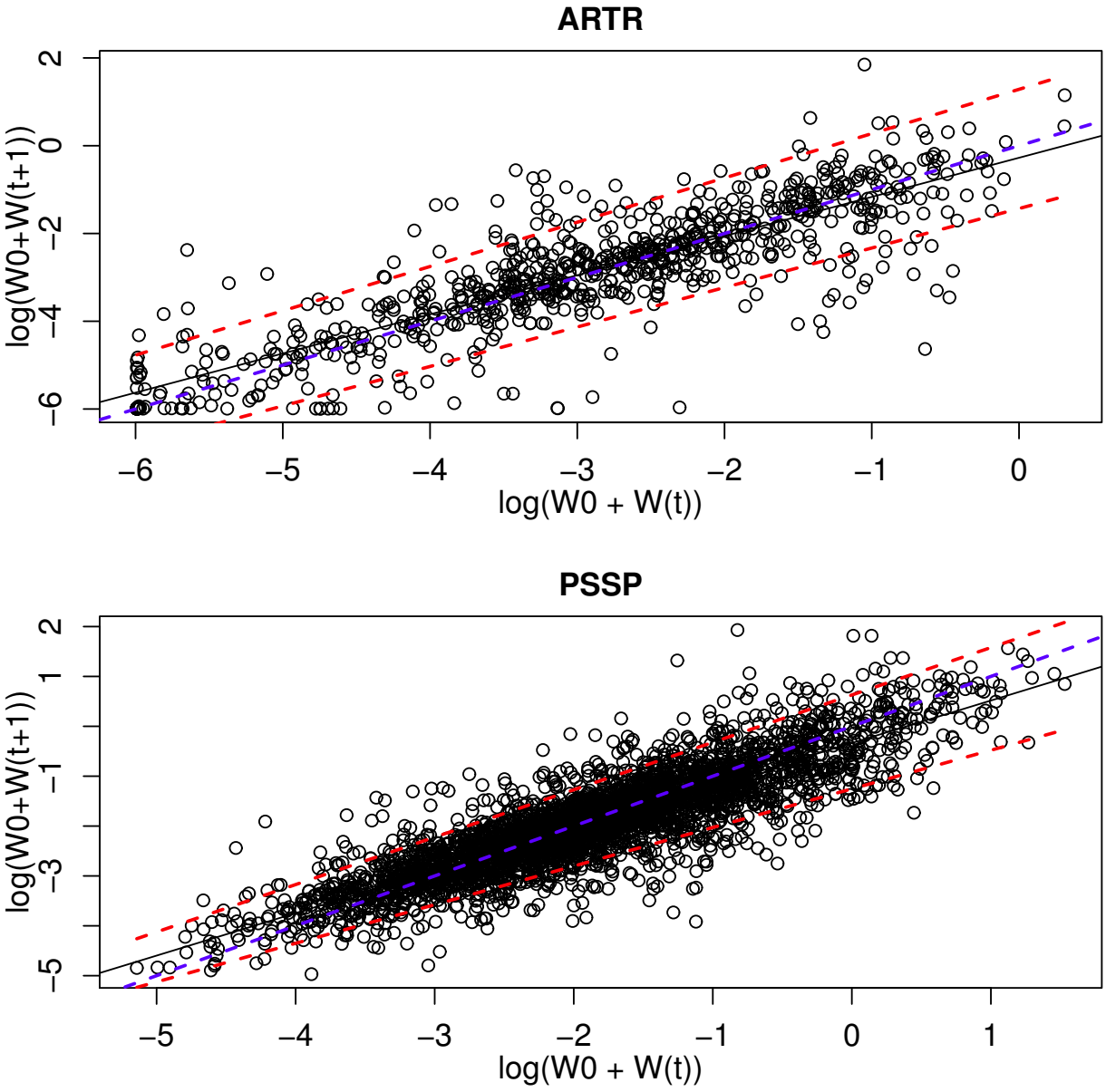

Figure C7: [Figure C7 caption here.]

D Analysis of partitioning by W in the perennial plant IPMs

Preliminaries

We use the following notation:

- W_1: competition at birth (age 1).
- W_2: competition at age 2 (assuming you survive that long).
- Z: size at age 2 (assuming the plant survives to age 2). The model assumes that Z is independent of W_1 and W_2.
- B: Bernoulli random variable that is 1 with probability $s(W_1)$, the probability of surviving to age 2 given competition W_1.
- R^*: lifetime reproductive success, conditional on surviving to year 2.
- $R = BR^*$: lifetime reproductive success.

The probability density function of the random variable X is $f_X(x)$ (we use upper case letters for random variables and lower case for possible values of a random variables); $f_{X|Y}(x|y)$ is the conditional density function of X given that $Y = y$. Density functions can include Dirac δ functions representing discrete outcomes.

We can imagine that at birth individuals are assigned values of Z and W_1 (independent draws from their respective distributions), assigned a value of W_2 from the conditional distribution of W_2 given W_1, and assigned an R^* value from the conditional distribution of R^* given W_2 and Z. Thus Z and R^* "exist" for all individuals, but they are relevant only if $B = 1$.

It is important to note that conditional on W_1, B and R^* are independent. Given $W_1 = w_1$, B is Bernoulli with parameter $s(W_1)$, and R^* is drawn from the distribution

$$f_{R^*|W_1}(r^*|w_1) = \iint f_{R^*|(Z,W_2)}(R^*|Z = z, W_2 = W_2) f_Z(z) f_{W_2|W_1}(W_2|w)\, dW_2\, dz.$$

Partitioning

The overall partitioning is

$$Var(R) = \mathbb{E}_{W_1}(Var(R|W_1)) + Var_{W_1}(\mathbb{E}(R|W_1)). \tag{S1}$$

If we take W_1 as the sole trait and regard every subsequent difference between individuals as luck, then (S1) partitions variance in LRS into luck (the first term) and trait variation (the second term).

However, we can further decompose the luck term in (S1) into several different aspects of luck. Tunneling down one level,

$$Var(R|W_1) = Var(BR^*|W_1) = \mathbb{E}_Z(Var(BR^*|W_1, Z)) + Var_Z(\mathbb{E}(BR^*|W_1, Z)). \tag{S2}$$

Because B and R^* are independent conditional on W_1, the terms in the right-hand side of (S2) can both be separated into first-year survival (B) and subsequent reproduction (R^*) components. In the first term in (S2) we have

$$\begin{aligned}
&Var(BR^*|W_1, Z) \\
&= (\mathbb{E}\, B|W_1)^2\, Var(R^*|W_1, Z) + Var(B|W_1)(\mathbb{E}\, R^*|W_1, Z)^2 + Var(B|W_1)\, Var(R^*|W_1, Z) \\
&= s^2(W_1)\, Var(R^*|W_1, Z)) + s(W_1)(1 - s(W_1))(\mathbb{E}(R^*|W_1, Z))^2 + s(W_1)(1 - s(W_1))\, Var(R^*|W_1, Z) \\
&= s(W_1)\, Var(R^*|W_1, Z) + s(W_1)(1 - s(W_1))(\mathbb{E}(R^*|W_1, Z))^2.
\end{aligned} \tag{S3}$$

In the second term in (S2),

$$\begin{aligned}
\mathbb{E}(BR^*|W_1, Z) &= \mathbb{E}(B|W_1, Z)E(R^*|W_1, Z) = s(W_1)\, \mathbb{E}(R^*|W_1, Z), \\
\text{so } Var_Z\, \mathbb{E}(BR^*|W_1, Z) &= s(W_1)^2\, Var_Z\, E(R^*|W_1, Z).
\end{aligned} \tag{S4}$$

Putting it all together (substituting (S3) and (S4) into (S2) and then (S2) into (S1)),

$$\begin{aligned}
Var(R) = &\underbrace{\mathbb{E}_{W_1,Z}[s(W_1)\, Var(R^*|W_1, Z)]}_{①} + \underbrace{\mathbb{E}_{W_1,Z}[s(W_1)(1 - s(W_1))(\mathbb{E}(R^*|W_1, Z))^2]}_{②} \\
&+ \underbrace{\mathbb{E}_{W_1}[s(W_1)^2\, Var_Z\, E(R^*|W_1, Z)]}_{③} + \underbrace{Var_{W_1}[\mathbb{E}(R|W_1)]}_{④}.
\end{aligned} \tag{S5}$$

The interpretation of these terms is explained in the main text, after equation 8.

A Simple Example

As a check on the calculations we consider a simple example where $Var(R)$ can be simulated and compared to the sum of the terms in the partitioning. Happily, the results are consistent with the hypothesis that our math is correct. The example is as follows:

- $W_1 = 1$ or 2 with equal probability.
- Survival to age 2 occurs with probability s_j if $W_1 = j$, with $s_1 > s_2$.
- Size age 2 is $Z = 5$ or 10, with $g = Prob(Z = 10)$ as a parameter.
- W_2, the value of W_1 at age 2, equals W_1 or $W_1 - 1$ with equal probability.
- Conditional on survival to age 2, lifetime reproductive success R^* is Poisson$(Z - W_2)$
- We let $p_{ij} = p_i^{(W_1)} p_j^{(Z)}$ denote the probability that $W_1 = i, Z = j$.

1. Term ① is $\sum_{i,j} p_{ij} s_i\, Var(R^*|W_1 = i, Z = j)$. Given that $W_1 = i$, W_2 is i or $i - 1$ with equal probability, so R^* is Poisson$(j - i)$ or Poisson$(j - i + 1)$ with equal probability. We can use the following special case of the variance decomposition: if $X = AX_1 + (1 - A)X_2$ where A, X_1, X_2 are independent random variables and A is Bernoulli with success probability a, then
$$Var\, X = a\, Var\, X_1 + (1 - a)\, Var\, X_2 + a(1 - a)(\mathbb{E}\, X_1 - \mathbb{E}\, X_2)^2.$$

The case at hand is the conditional distribution $R^* \sim APois(j-i) + (1-A)Pois(j-i+1)$ with $a = 0.5$ so we have

$$Var(R^*|W_1 = i, Z = j) = 0.5(j-i) + 0.5(j-i+1) + 0.25 = j - i + 0.75$$

and so

$$\text{Term } ① = \sum_{i,j} p_{ij} s_i (j - i + 0.75).$$

2. In term ②, $R^* \sim Pois(Z - W_2)$ and W_2 equals W_1 or $W_1 - 1$ with equal probability independent of Z, so

$$\mathbb{E}(R^*|W_1, Z) = \frac{1}{2}[(Z - W_1) + (Z - (W_1 - 1))] = Z - W_1 + 0.5. \tag{S6}$$

The integrand in ② (the quantity in square brackets) is therefore $s(W_1)(1 - s(W_1))(Z - W_1 + 0.5)^2$, so its expectation with respect to the distribution of Z and W_1 is

$$\text{Term } ② = \sum_{i,j} p_{ij} s_i (1 - s_i)(j - i + 0.5)^2.$$

3. For term ③, using (S6) we have

$$Var_Z[\mathbb{E}(R^*|W_1, Z)] = Var_Z[Z - W_1 + 0.5] = Var_Z(Z) = 25g(1-g).$$

Thus

$$\text{Term } ③ = \mathbb{E}_{W_1}[s(W_1)^2 25g(1-g)] = 0.5(s_1^2 + s_2^2) \times 25g(1-g).$$

4. For term ④, because B and R^* are conditionally independent given W_1, we have $\mathbb{E}(BR^*|W_1) = \mathbb{E}(B|W_1)\,\mathbb{E}(R^*|W_1)$. Since B is Bernoulli, $\mathbb{E}(B|W_1 = i) = s(i)$. Given that $W_1 = i$, W_2 equals i or $i - 1$ with equal probability so $R^* \sim Pois(Z - W_2)$ has mean $\mathbb{E}(Z) - (i - 0.5) = 5.5 + 5g - i$. We therefore have

$$\mathbb{E}(R|W_1 = i) = \mathbb{E}(B|W_1 = i)\,\mathbb{E}(R^*|W_1 = i) = s(i)(5.5 + 5g - i). \tag{S7}$$

Thus, $\mathbb{E}(R|W_1)$ has two possible values with equal probability, the right-hand side of (S7) with $i = 1$ or $i = 2$. Call these r_1 and r_2. So $\mathbb{E}(R|W_1)$ is distributed as $r_2 + [(r_1 - r_2)Bernoulli(0.5)]$, and its variance is

$$\text{Term } ④ = 0.25(r_1 - r_2)^2 = 0.25(s_1(4.5 + 5g) - s_2(3.5 + 5g))^2.$$

Figure S1 confirms that estimates of $Var(R)$ from simulating the model are very close to the sum of the terms in the partition, computed by a mix of simulation (terms 1 and 2) and analytic calculation (terms 3 and 4). So it works!

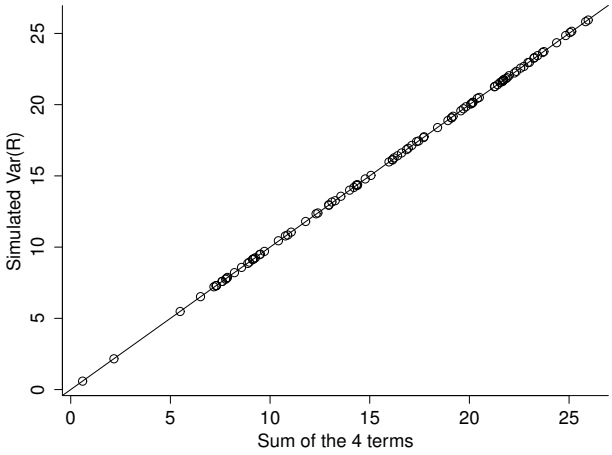

Figure S1: [Figure S1 caption here.]

Computing the terms for the perennial plant IPMs

Computing the terms in eq. (S5) takes some care because W_1 happens at age 1 and Z happens at age 2. For greater clarity, what has been called Z will be called Z_2 in this section. We also switch the order of z and w in conditional expectations (size first, "quality" W second) to match our R scripts for these models and the material on size-quality models in Ellner et al. (2016). The calculations are done in `Rpartition/empirical/PartitionByW.R`.

We use the setup described in Supplemental Information section *Constructing the IPM iteration matrix*. There are `mx` mesh points in vector `yx` for size, and `mW` mesh points in vector `yW` for W. The state vector for age 2 and above has length `mx*mW` in the sequence produced by `expand.grid` applied to the size and W mesh points. To this is pre-pended `mW` mesh points for seedlings, classified only by W. The IPM is implemented with $log(W_0 + W)$ rather than W as the state the variable. All demographic rate functions in the R code back-transform to W before applying the fitted demographic models. The iteration matrix for the full IPM is

$$K = \begin{pmatrix} 0 & F_2 \\ P_1 & P_2 \end{pmatrix} = P + F. \tag{S8}$$

(Matrix P is K with F_2 zeroed out, F is K with P_1 and P_2 zeroed out). The upper-left 0 matrix is size `mW` by `mW`. Block P_1 (`mx*mW` by `mW`) is the survival-growth matrix for seedlings; P_2 (`mx*mW` by `mx*mW`) is the survival-growth matrix for age-2 and older individuals; F_2 (`mW` by `mx*mW`) is the fecundity of age-2 and older individuals, and `yx,yW` are the meshpoints for size and competition.

A few other things we need here:

1. Let $f_Z(z)$ denote the probability density of Z_2, and $f_W(w)$ denote the probability density of W_1. These are the initial state distributions. Let $p_Z(i)$, $p_W(j)$ denote the discrete probability distributions of Z_2 and of W_1 on the meshpoints, scaled so their sum is 1. In the IPM code, we make the vectors

```
pZ = c2_x1(yx,pars); pZ = pZ/sum(pZ); # size
pW = c1_w1(yW,pars); pW = pW/sum(pW); # competition
```

2. Let $s_W(j)$ denote survival probability of seedlings at the jth W meshpoint. In the code, this is a vector

```
sW = s_seed(yW,pars)
```

3. Methods from Chapter 3 of Ellner et al. (2016), applied to P_2, can give $\mathbb{E}(R^*|Z_2 = z, W_2 = w)$ and $\mathbb{E}(R^{*2}|Z_2 = z, W_2 = w)$ as functions of z and w, because these are about the LRS of a 2-year-old with "initial" state $(Z_2 = z, W_2 = w)$. We assume that these have been calculated and stored in matrices `RStar22` and `RstarSqr22`, respectively of dimension `mx` by `mW`. The `22` indicates that the expected values are conditional on values of Z_2 and W_2.

4. Let $q(w', w)$ denote the transition density for W, and `Q` the corresponding midpoint rule transition matrix for W. In terms of the code `IdahoIPMFunctions.R` code,

```
Q[i,j] = hW*g_w1w(yW[i],yW[j],pars)
```

Term ④ is the easiest. Let $N_2 = (I - P_2)^{-1}$ denote the fundamental operator for age 2^+ individuals. Let b be a vector of state-dependent per-capita fecundity for age 2 or older individuals (length of b =`mx*mW`). bN_2 is therefore the $\mathbb{E}(R^*)$ as a function of state at age 2. So in the IPM code, let e_i be a vector of length `mW` consisting of all zeros except for 1 in the i^{th} location. Then $bN_2P_1e_i$ is the expected value of $R = BR^*$ for an individual with W_1 equal to the i^{th} W meshpoint, because multiplication by P_1 accounts for age-1 mortality and the distribution of W_2 for survivors. Consequently,

$$\mathbb{E}(R|W_1) = bN_2P_1. \tag{S9}$$

Both sides of this equation are functions of W_1; in the code, a vector of length `mW` giving $\mathbb{E}(R|W_1)$ for W_1 at the meshpoints. Let's call this vector `ERW1`. Then

$$④ = \texttt{ sum(pW*(ERW1\^2)) - sum(pW*ERW1)\^2} \tag{S10}$$

Note that `sum(pW*ERW1)` is R_0, so (as a sanity check) it has to equal R_0 computed the usual way from the P and F matrices. In our code, per-capita fecundity is scaled so that $R_0 = 1$.

For terms ① − ③ we need the conditional mean and variance of R^* given Z_2 and W_1. So the quantities we need are $\mathbb{E}(R^*|Z_2 = z, W_1 = w)$ and $\mathbb{E}(R^{*2}|Z_2 = z, W_1 = 2)$ for all (w, z) meshpoints. We can get the mean using

$$\mathbb{E}(R^*|Z_2 = z, W_1 = w) = \int \mathbb{E}(R^*|Z_2 = z, W_2 = w')q(w', w)dw'. \tag{S11}$$

For the meshpoints, this says that `Rstar21[i,j]` $= \sum_k$ `Rstar22[i,k]Q[k,j]` This is compactly written as

$$\texttt{Rstar21 = Rstar22 \%*\% Q} \tag{S12}$$

Sanity check: the dimensions of these are `(mx by mW)` = `(mx by mW)` × `(mW by mW)`, which works. Exactly the same thing works for $\mathbb{E}(R^{*2}|Z_2 = z, W_1 = w)$:

$$\begin{aligned}&\texttt{RstarSqr21 = RstarSqr22 \%*\% Q and then}\\ &\texttt{VarRstar21 = RstarSqr21 - (Rstar21\^2)}\end{aligned} \tag{S13}$$

Here `VarRstar21` is the matrix of values of $Var(R^*|Z_2 = z, W_1 = w)$. With this, and values of the conditional mean of R^* in `Rstar21`, we're ready to go.

Term ① is $\int\int f_W(w) f_z(z) s(w)\, Var((R^*|Z_2 = z, W_1 = w) dw dz$. In the IPM code this is the sum of the matrix whose i, j entry is `pZ[i]*pW[j]*sW[j]*VarRstar21[i,j]`.

Term ② is, similarly, the sum of the matrix whose i, j entry is
`{pZ[i]*pW[j]*sW[j]*(1-sW[j])*(Rstar21[i,j]^2)}`.

Term ③ is just a bit more complicated. $Var_Z\, E(R^*|Z_2, W_1)$ means take the values `Rstar21[1:mx,j]` corresponding to one value of W_1, and compute their variance under the distribution of Z_2. That is, for $j = 1, 2, \ldots,$ `mW` do

```
VarZvals[j] = sum(pZ*(Rstar21[1:mx,j]^2)) - sum(pZ*Rstar21[1:mx,j])^2.
```

Then term ③ is

```
sum(pW*(sW^2)*VarZvals)
```

and we're done.

E Quantifying selection when fitness is a random variable

This derivation is modeled after Rice (2008). Notation:

- $\mathbb{E}\, x$ and $\hat{x}$: expected value of x
- $\bar{x}$: mean of x over a population
- w_j: the (random) number of offspring of individual j
- z_j: size of individual j
- x_j: phenotype of individual j
- N: population size

Assume that all offspring have the same phenotype as their parent. The expected mean phenotype next generation is

$$\mathbb{E}\, \bar{x}(t+1) = \mathbb{E}\left(\frac{\sum_{j=1}^N w_j x_j}{\sum_{j=1}^N w_j}\right) = \mathbb{E}\left(\frac{\frac{1}{N}\sum_{j=1}^N w_j x_j}{\frac{1}{N}\sum_{j=1}^N w_j}\right). \tag{S14}$$

Write the number of offspring of individual j as the expected number of offspring for phenotype x_j plus a potentially large noise term ϵ_j. We assume that the random component of fitness, ϵ_j, is independent of the trait and identically distributed across individuals. We then Taylor expand $\widehat{w}(x_j)$ about the mean phenotype, $\bar{x}$:

$$w_j = \widehat{w}(x_j) + \epsilon_j \approx \widehat{w}(\bar{x}) + \widehat{w}'(\bar{x})(x_j - \bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})(x_j - \bar{x})^2 + \epsilon_j. \tag{S15}$$

The numerator in eq. S14 is

$$\frac{1}{N}\sum_j x_j w_j = \frac{1}{N}\sum_j (x_j-\bar{x})\widehat{w}(x_j) + \frac{1}{N}\bar{x}\sum_j \widehat{w}(x_j) + \frac{1}{N}\sum_j x_j\epsilon_j \tag{S16}$$

$$\approx \frac{1}{N}\sum_j (x_j-\bar{x})\left(\widehat{w}(\bar{x}) + \widehat{w}'(\bar{x})(x_j-\bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})(x_j-\bar{x})^2\right)$$

$$+ \frac{1}{N}\bar{x}\sum_j \left(\widehat{w}(\bar{x}) + \widehat{w}'(\bar{x})(x_j-\bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})(x_j-\bar{x})^2\right) + \frac{1}{N}\sum_j x_j\epsilon_j.$$

We assume that the trait x has a distribution with mean $\bar{x}$ and variance $Var(x)$. This causes eq. S16 to become

$$\frac{1}{N}\sum_j x_j w_j \approx \widehat{w}'(\bar{x})\, Var(x) + \bar{x}\left[\widehat{w}(\bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})\, Var(x)\right] + \overline{x\epsilon}. \tag{S17}$$

Meanwhile, the denominator is

$$\frac{1}{N}\sum_j w_j \approx \widehat{w}(\bar{x}) + \frac{1}{N}\sum_j \left(\widehat{w}'(\bar{x})(x_j-\bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})(x_j-\bar{x})^2 + \epsilon_j\right) \tag{S18}$$

$$= \widehat{w}(\bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})\, Var(x) + \bar{\epsilon}. \tag{S19}$$

Set $A = \widehat{w}(\bar{x}) + \frac{1}{2}\widehat{w}''(\bar{x})\, Var(x)$. We then have

$$\frac{\frac{1}{N}\sum_{j=1}^N w_j x_j}{\frac{1}{N}\sum_{j=1}^N w_j} \approx \frac{\widehat{w}'(\bar{x})\, Var(x) + \bar{x}A + \overline{x\epsilon}}{A + \bar{\epsilon}}. \tag{S20}$$

The approximation in (S20) comes from assuming that trait variation is small. However fitness variation ϵ_j is $O(1)$ — we do not assume that the random variation in fitness around its expected value (given the trait) is small. However, $\bar{\epsilon}$ is the mean of N independent random variables with (by definition) zero mean, and therefore is $O(N^{-1/2})$ with mean 0. Similarly $\overline{x\epsilon}$ is $O(N^{-1/2})$ with expected value $\mathbb{E}(1/N)\sum_j x_j\epsilon_j = (1/N)\sum_j x_j\,\mathbb{E}\,\epsilon_j = 0$.

For large N we can therefore take $\bar{\epsilon}$ as a small parameter in (S20) to get

$$\frac{\frac{1}{N}\sum_{j=1}^N w_j x_j}{\frac{1}{N}\sum_{j=1}^N w_j} \approx \frac{\widehat{w}'(\bar{x})\, Var(x) + \bar{x}A + \overline{x\epsilon}}{A}\left(1 - \frac{\bar{\epsilon}}{A} + \frac{\bar{\epsilon}^2}{A^2}\right). \tag{S21}$$

Combining equations (S14) and (S21) and taking expectations of both sides, we have that to $O(N^{-1})$

$$\mathbb{E}\,\bar{x}(t+1) = \frac{\widehat{w}'(\bar{x})\, Var(x) + \bar{x}A}{A}\left(1 + \frac{1}{A^2}\,\mathbb{E}(\bar{\epsilon}^2)\right) - \frac{1}{A^2}\,\mathbb{E}(\overline{x\epsilon}\;\bar{\epsilon}). \tag{S22}$$

Moreover

$$\mathbb{E}(\bar{\epsilon}^2) = \mathbb{E}\left(\frac{1}{N^2}\sum_j \epsilon_j \sum_k \epsilon_k\right) = \mathbb{E}\left(\frac{1}{N^2}\sum_j \epsilon_j^2\right) = \frac{1}{N^2}\sum_j \mathbb{E}\,\epsilon_j^2 = \frac{1}{N}\,Var(\epsilon) = \frac{1}{N}\,Var(w|x) \tag{S23}$$

and

$$\mathbb{E}(\overline{x\epsilon}\,\overline{\epsilon}) = \mathbb{E}\left(\frac{1}{N^2}\sum_j x_j\epsilon_j\sum_k \epsilon_k\right) = \mathbb{E}\left(\frac{1}{N^2}\sum_j x_j\epsilon_j^2\right) = \frac{1}{N^2}\sum_j x_j\,\mathbb{E}\,\epsilon_j^2 \tag{S24}$$
$$= \frac{1}{N^2}\sum_j x_j\,Var(\epsilon) = \frac{1}{N}\bar{x}\,Var(\epsilon) = \frac{1}{N}\bar{x}\,Var(w|x),$$

where $Var(w|x) = Var(\epsilon)$ is the random variation in fitness around its expected value given the trait. Substituting the last two equations into (S22) we have

$$\mathbb{E}\,\bar{x}(t+1) \approx \frac{\widehat{w}'(\bar{x})\,Var(x) + \bar{x}A}{A}\left(1 + \frac{1}{A^2}\frac{1}{N}\,Var(w|x)\right) - \frac{1}{A^2}\frac{1}{N}\bar{x}\,Var(w|x), \tag{S25}$$

which can be re-written as

$$\mathbb{E}\,\Delta\bar{x} \approx \frac{\widehat{w}'(\bar{x})}{A}\,Var(x)\left(1 + \frac{1}{A^2N}\,Var(w|x)\right). \tag{S26}$$

Note that the first term is the usual measure of selection for small trait variance and the second is a correction that accounts for the fact that fitness is a random variable.

We can also use (S21) to approximate the "random drift" component of selection that results from random variation in w_j unrelated to trait differences. Specifically, we want to approximate the variance of $\Delta\bar{x}$ conditional on the initial state of the population, meaning that we treat the x_j as given constants, while the ϵ_j are random with variance $Var(w)$. So only terms involving ϵ contribute variance to (S21). The leading-order random terms are those with $\overline{\epsilon}$ and $\overline{x\epsilon}$ on their own (while cross-terms of these with another random term are higher order in $N^{-1/2}$). So defining $c = \widehat{w}'(\bar{x})\,Var(x)/A$, the variance of $\Delta\bar{x}$ is therefore approximately the variance of

$$\frac{\overline{x\epsilon}}{A} - \frac{\overline{\epsilon}}{A}(\bar{x}+c) = \frac{\overline{x\epsilon} - \overline{\epsilon}(\bar{x}+c)}{A}. \tag{S27}$$

Note that

$$\overline{x\epsilon} - \overline{\epsilon}(\bar{x}+c) = \frac{1}{N}\sum_j x_j\epsilon_j - \frac{1}{N}\sum_j(\bar{x}+c)\epsilon_j = \frac{1}{N}\sum_j(x_j - \bar{x} - c)\epsilon_j. \tag{S28}$$

The terms in the last sum are independent random variables with variance $(x_j - \bar{x} - c)^2\,Var(\epsilon) = (x_j - \bar{x} - c)^2\,Var(w|x)$. The variance of (S28) is therefore $(Var(w|x)/N^2)$ times $\sum_j(x_j - \bar{x} - c)^2 = N(Var\,x + c^2)$. We are assuming that $Var\,x$ is small, so c^2 is negligible compared to $Var\,x$. We therefore get that

$$Var\,\Delta\bar{x} \approx \frac{Var(w|x)\,Var\,x}{A^2N}. \tag{S29}$$

As a sanity-check on the calculations, note that the approximation correctly predicts that $Var\,\Delta\bar{x} = 0$ if either $Var(w|x) = 0$ or $Var\,x = 0$. In the former situation drift is absent because fitnesses are nonrandom, so the trait change is a deterministic function of the current trait distribution. In the latter situation, all individuals are identical in trait value, so regardless of who has the kids, the trait mean in the next generation will equal the current trait mean.

F Supplemental figures

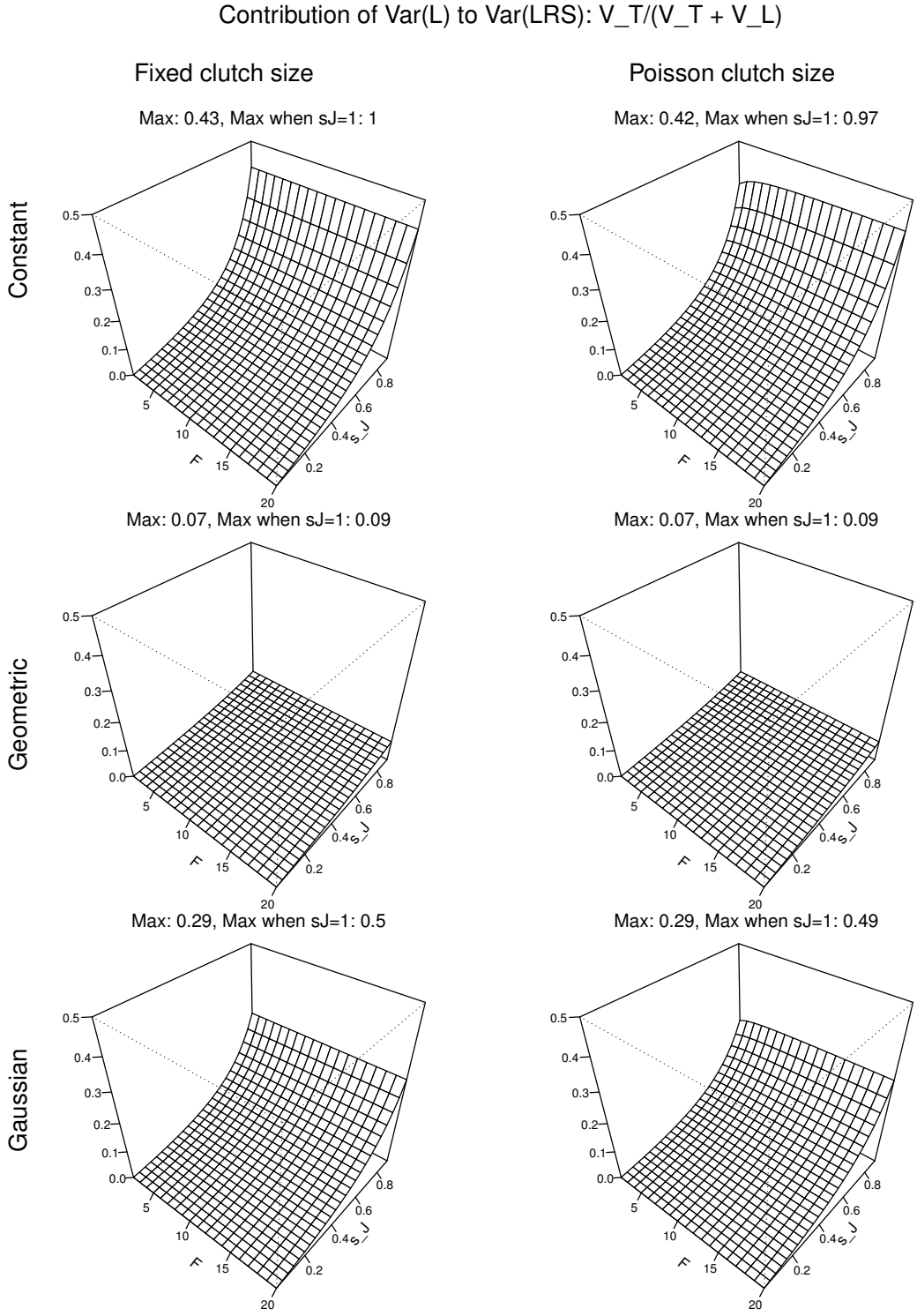

Figure S2: [Figure S2 caption here.]

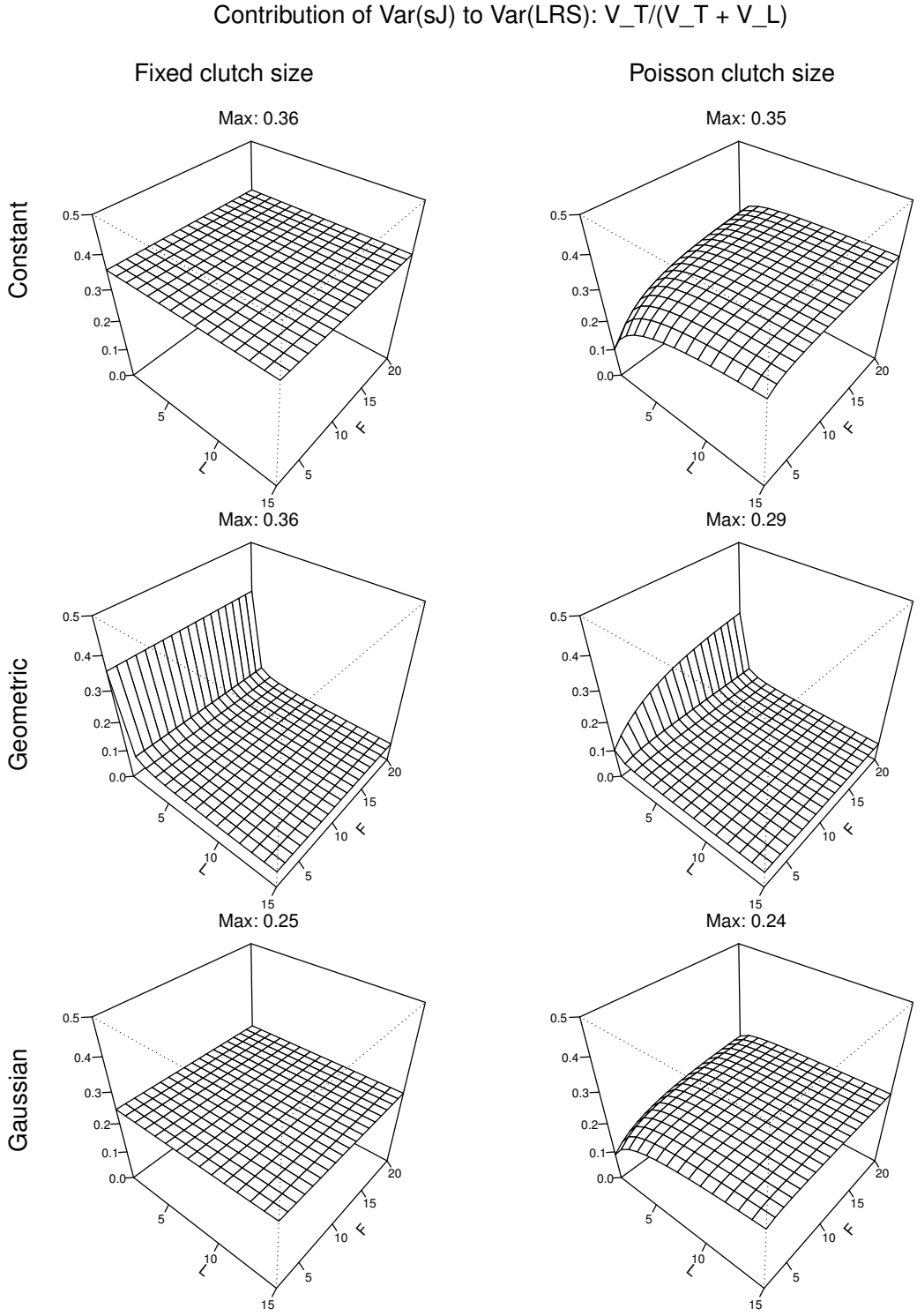

Figure S3: [Figure S3 caption here.]

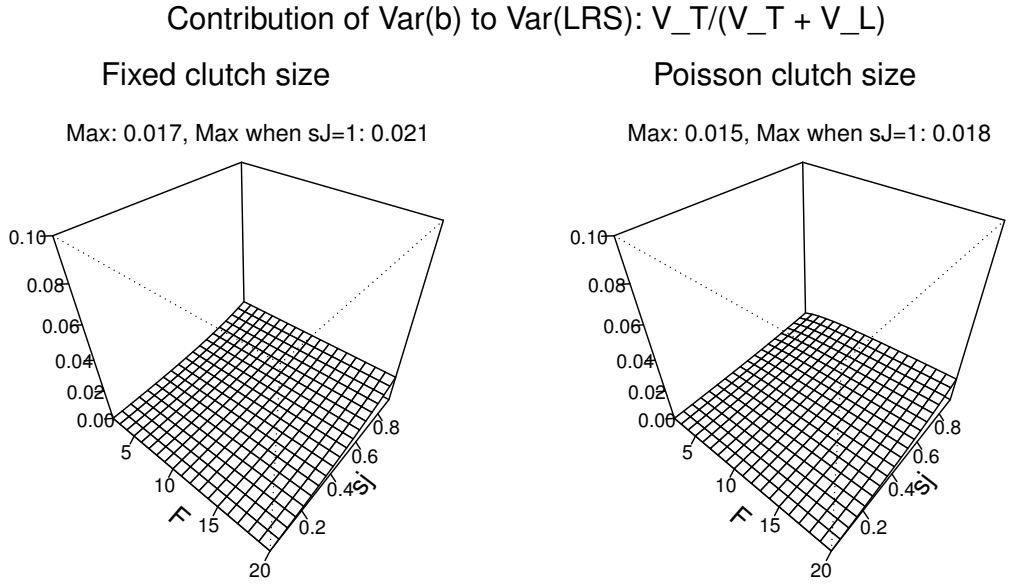

Figure S4: [Figure S4 caption here.]

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Figure legends

Figure 1: Relative contribution of trait variation, $V_{\mathbb{T}}/(V_{\mathbb{T}} + V_{\mathbb{L}})$ in the iteroparous two-stage model with $\overline{F} = 2$ and trait variation $CV_F = 0.3$. Lifespan L is constant, geometrically distributed, or Gaussian distributed with a CV of 0.3. These calculations do not rely on the small trait-variance approximation. Surfaces are plotted for survival to adulthood $s_J \leq 0.9$. Figure generated by `RpartitionItero.R`.

Figure 2: As in fig. 1 for the semelparous two-stage model with $\overline{F} = 2, d = 0.5, CV_F = 0.3$. These calculations do not rely on the small trait-variance approximation. Surfaces are plotted for survival to adulthood $s_J \leq 0.95$. Figure generated by `RpartitionSemel.R`.

Figure 3: Distribution of mean annual offspring number F conditional on lifetime reproductive success (LRS) for the two-stage model with F as the varying trait. Contour lines show probability densities. When lifetime is fixed, adults live 10 years; when lifetime is variable, there is an annual adult survival probability of 0.9. Variable trait F has mean 5 and CV 0.2. Figure generated by `TwoStageWinnerTraits2Plots.R`.

Figure 4: Trait distribution conditional on lifetime reproductive success (LRS) for the Kittiwake model. Contour lines show probability densities. The trait is an underlying quality index x affecting both survival and breeding probability. Survival for stages 2–5 is the logit transform of $b_a + x$, where b_a is an age-specific intercept, and quality index x is the same for all ages. Quality index is assumed to have a Gaussian distribution with mean 0 and CV estimated from the interquartile ranges of survival plotted in fig. 1 of Cam et al. (2002). The same trait also determines adult breeding probability. For adult birds (age$\geq$ 5), the probabilities of transitioning from any state into one of the breeder states (failed attempt, one chick, 2-3 chicks) are all multiplied by a factor ϕx, where the value of ϕ is chosen so that the resulting adult breeding probability in the stationary age-breeding state distribution has among-individual CV corresponding to the average interquartile ranges of breeding probability for ages 5-12 plotted in Figure 1 of Cam et al. (2002) assuming a Gaussian distribution. The LRS axis on the figure runs from the 5th to the 95th percentile of individual LRS in the model, including effects of trait variation. Source file: `empirical/KittiwakeWinnerTraitsFecSurv3.R`

Figure 5: Comparison of survival and growth trajectories for *Artemisia*(ARTR) individuals with different values of initial crowding W_1. The plotted curves in each panel go from the 5^{th} to the 95^{th} percentiles of the distribution of W_1, with smaller values being advantageous. A) Probability of survival from birth (age 1) to age a. B) Probability of survival from age a to age $a + 1$. "Annual mortality plateau" is 1 minus the asymptote of the annual survival curves (which was estimated by computing annual survival rates out age 100). C) Mean size, conditional on survival. D) Mean per-capita number of recruits, conditional on survival. Source file: `empirical/IdahoIPMLifeCycleStats.R`

Figure 6: As in fig. 5, for *Pseudoroegneria* (PSSP). Source file: `empirical/IdahoIPMLifeCycleStats.R`

Figure 7: A) Conditional distribution of initial crowding W_1, as a function of realized lifespan L for *Artemisia tridentata*. Contour lines show probability densities. B) Conditional mean of W_1 given L expressed as a z-score (i.e., the difference between the conditional and unconditional means of W_1, divided by the unconditional standard deviation); thus a value of $z = -1$ indicates a value of W_1 that is one standard deviation below the mean, in the distribution of W_1 for all seedlings. C) Conditional probability that initial crowding W_1 was above (i.e., worse than) the median value of W_1 for all seedlings. Figure generated by `empirical/IdahoWinnerTraits2Plots.R`

Figure 8: As in figure 7, for *Pseudoroegneria spicata*. Figure generated by `empirical/IdahoWinnerTraits2Plots.R`

Figure 9: Plots of the size- and quality-dependence of A) survival, B) mean per-capita fecundity, C),D) mean growth rate, in the prototype size-structured model, for the two parameter sets in Table B1 (Set 1:black, Set2:gray). Size can be negative because we assume a log-transformed size measure. Solid line in each panel is the rate function for quality $q = 0$, dashed lines are for $q = \pm 1$, which is ± 1 standard deviations of the assumed quality distribution in the population. In C) and D) the point where the solid line intersects the 1:1 line (dot-dash, red online) is the asymptotic individual size in the absence of random variability in growth dynamics. Figure generated by `SizeQualityFunctionsPlot.R` scripts that it sources.

Figure 10: Plots of age-dependent A) survival, B) mean size, and C) mean fecundity for the size-quality IPM with the parameters in the first row of Table B1. Curves run from the 5th to the 95th percentiles of quality q, with the mean (and median) value $q = 0$ plotted as the heavy black line. Panel D) shows R_0 as a function of q. Figure generated by `SizeQualityFunctions.R` and `SizeQualityVarPartition.R`.

Figure 11: Same as the previous figure, for the parameters in the second row of Table B1. Figure generated by `SizeQualityFunctions.R` and `SizeQualityVarPartition.R`.

Figure 12: Plots showing how terms in the variance partition for the prototype size-structured model are affected by mean lifespan, for the parameters in the top row of Table B1 (relatively short expected lifespan with high per-capita annual fecundity). Figure generated by `SizeQualityFunctions.R` and `SizeQualityVarPartition.R`.

Figure 13: Same as the previous figure, for the parameters in the second row of Table B1 (longer life with lower annual fecundity). Figure generated by `SizeQualityFunctions.R` and `SizeQualityVarPartition.R`.

Figure 14: Distribution of $\log(W)$ at age 1 for different classes of individuals in ARTR: all likely seedlings, likely seedlings that survive to age 2, and individuals that are not likely seedlings. The bottom-right panel is the prediction for seedlings that survive to age 2, generated by drawing a bootstrap sample of size 500,000 from the likely seedlings, applying the fitted survival model to each bootstrapped observation (with a coin toss for live or die), and plotting the W values of "survivors." The fitted survival model includes random year and Group effects, and random slopes on W. Source file: `Fit_survival_seedlings.R`

Figure 15: As in the previous Figure, for HECO.

Figure 16: As in the previous Figure, for POSE.

Figure 17: As in the previous Figure, for PSSP.

Figure 18: Distribution of size (log area) for seedlings that survive to age 2. The solid black line is a kernel density estimate calculated from the observed sizes, with a bandwidth of 0.2. The dashed (blue) line is the fitted mixture of two Gaussian distributions. Source file: `Fit_Growth_Seedlings.R`

Figure 19: Comparisons of predicted subsequent size of older individuals from the linear mixed-effects models used in the IPM, a model that adds a quadratic effect of initial size, and a model that adds spline responses to initial size and to W fitted using `gam`. Each curve shows average size (logarea) at time $t+1$ for the 0-10%,11-20%, etc. quantiles of initial size, for the data (solid black circles) and for sizes predicted by the three models (open circles). Source file: `Fit_Growth_Older_GAM.R`

Figure 20: Plot of $W(t+1)$ versus $W(t)$ for ARTR and PSSP, on log-transformed scale with offset parameter $W_0 = 0.0025$ corresponding to one new recruit at a distance where its impact is reduced by 99%. Solid black line is the fitted linear regression; dashed red lines are the 5th and 95th percentiles of the fitted Student-t distribution of residuals with nonconstant variance. The dashed blue line is the 1:1 line. Source file: `ModelingW.R`

Figure 21: Comparison of simulated $Var\,R$ with the sum of terms in the decomposition, for the simple example. Circles are the results for 100 randomly generated parameter sets (simulating 500000 individuals at each parameter set), and the line is the 1:1 line. Source file: `SimplePartitionSimulate.R`

Figure 22: Relative contribution of trait variation, $V_{\mathbb{T}}/(V_{\mathbb{T}} + V_{\mathbb{L}})$ in the iteroparous two-stage model with $\overline{L} = 20$ and trait variation $CV(L) = 0.3$. Lifespan is constant, geometrically distributed, or Gaussian distributed with a CV of 0.3. These calculations do not rely on the small trait-variance approximation. Figure generated by `RpartitionItero.R`. Surfaces are plotted for survival to adulthood $s_J \leq 0.9$.

Figure 23: Relative contribution of trait variation, $V_{\mathbb{T}}/(V_{\mathbb{T}} + V_{\mathbb{L}})$ in the iteroparous two-stage model with $\overline{s}_J = 0.8$ and trait variation $CV(s_J) = 0.3$. Lifespan is constant, geometrically distributed, or Gaussian distributed with a CV of 0.3. These calculations do not rely on the small trait-variance approximation. Figure generated by `RpartitionItero.R`.

Figure 24: Relative contribution of trait variation, $V_{\mathbb{T}}/(V_{\mathbb{T}} + V_{\mathbb{L}})$ in the semelparous two-stage model with $\overline{b} = 0.8$ and trait variation $CV(b) = 0.3$. The probability of dying without reproducing, d, is 0.5. Surfaces are plotted for survival to adulthood $s_J \leq 0.9$. These calculations do not rely on the small trait-variance approximation. Figure generated by `RpartitionSemel.R`.