

1 **TITLE**

2 Toward a General Theory of Heteromorphic Reproduction

3

4 **AUTHORS**

5 P. William Hughes^{1,2*}

6

7 **AUTHOR AFFILIATIONS**

8 1 University of Cambridge, Cambridge, UK

9 2 European Graduate School, Saas-Fee, Switzerland

10

11 *Corresponding author: P. William Hughes

12 Email: pwh29@cam.ac.uk

13

14 Manuscript type: Original Article

15

ABSTRACT

Organisms often divide reproductive investment among outputs that differ in morphology, timing, or reproductive mechanism. In this paper I extend the minimum-risk treatment of seed heteromorphism to the more general question of organisms with ‘portfolios’ of biologically distinct reproductive outputs. The resulting framework specifies a common investment and fitness currency, calculates returns and covariances across shared environmental states, and compares minimum variance at fixed expected fitness with maximization of long-run geometric growth.

I then derive general inclusion criterion for an additional output and provide an analysis of two seed morphs and a clonal propagule present in four hypothetical environments. For this result, an expected return of three results in the clone reduces minimum variance by 83.6%. When both systems are optimized independently for geometric growth, the clone enters despite lower standalone arithmetic and geometric returns than the optimized seed-only portfolio, with the geometric mean growth rising by 5.2% even as arithmetic mean return falls. Overall, these illustrative calculations demonstrate the usefulness of this framework, since it provides an explicit procedure for showing how different reproductive outputs must perform as one portfolio, illustrates how to compare portfolios, and can be used to develop allocation predictions.

KEYWORDS

reproductive heteromorphism; reproductive allocation; portfolio theory; clonal reproduction; environmental variation; geometric mean fitness

INTRODUCTION

Organisms can produce more than one kind of reproductive output. These outputs may differ in size or morphology (Smith and Fretwell, 1974; Imbert, 2002; Scholl et al., 2020; Chen and Giladi, 2020), disperse over different distances (Venable and Brown, 1988; Bonte et al., 2012), remain dormant for different periods (Baskin and Baskin, 2014; Lennon et al., 2021), or enter the environment at different times (Cohen, 1966; Koons et al., 2008; ten Brink et al., 2020). Some organisms also divide reproductive investment between sexual offspring and clonal propagules (Vallejo-Marín et al., 2010; Barrett, 2015; Yang and Kim, 2016). These routes need not succeed under the same environmental conditions (Venable and Brown, 1988; Starrfelt and Kokko, 2012). They therefore raise a question that cannot be answered by examining each output separately: how should an organism allocate finite reproductive resources among alternatives whose successes vary together or independently?

In this paper I propose to treat this as a reproductive portfolio strategy problem. For any set of available reproductive outputs (live offspring, seeds, stolons, spores, eggs, etc.) the portfolio defines the fraction of investment allocated to each, and each output can then be evaluated using a cost and a fitness return that can change with the environment. The performance of a strategy therefore depends on its allocation, individual returns, and the relationships among those returns. Furthermore, an output with modest average success may contribute disproportionately when the remaining portfolio performs poorly. Conversely, a productive output may offer little diversification when it fails under the same conditions as the others (Real, 1980; Venable and Brown, 1988). I consequently evaluate each output as part of a complete reproductive portfolio, considering both risk and long-run growth.

Much of the background I use is not new; tracking environmental variation has long shaped theory about reproduction and life-history decisions. Cohen (1966) examined reproductive timing in fluctuating environments, and work on seed dormancy, dispersal, and heteromorphism described diversification across time and space (Venable and Lawlor, 1980; Venable, 1985; Venable and Brown, 1988; Imbert, 2002; Gianella et al., 2021). Real (1980) explicitly linked uncertainty, negatively covarying behaviors, and diversification. Frank and Slatkin (1990) separated levels of reproductive variance and their correlations; Yoshimura and Clark (1991) and Haccou and Iwasa (1995) developed stochastic optimality and mixed-strategy models. Later treatments clarify the roles of means, variances, and correlations and the empirical difficulty of inferring bet hedging from observed mixtures (Seger and Brockmann, 1987; Philippi and Seger, 1989; Childs et al., 2010; Simons, 2011; Starrfelt and Kokko, 2012). A phylogenetic comparison also links seed heteromorphism to aridity-related environmental variation, without establishing that every mixture is bet hedging (Scholl et al., 2020). These studies establish that neither covariance nor geometric mean fitness is new. The question I address is how to calculate them for outputs that differ in reproductive mechanism and demographic timing, using a single empirically accountable investment and return scale.

Two related criteria are needed to evaluate reproductive portfolios. Variance describes how widely reproductive return fluctuates around its mean; for multiplicatively growing lineages, expected logarithmic growth describes long-run performance across fluctuating generations (Lewontin and Cohen, 1969; Philippi and Seger, 1989; Starrfelt and Kokko, 2012). A strategy with low variance need not maximize long-run growth, particularly if its average return is also low (Yasui, 2022). In a previous paper, (Hughes, 2018) I developed minimum-risk allocation rules for two or more seed morphs and described the attainable fitness–risk combinations. That study also anticipated extending the comparison to sexual seeds and

vegetative propagules. Subsequent theoretical work has investigated how seasonal uncertainty, seedling competition, and adult survival jointly shape the evolution of early- and late-germinating seed strategies in perennials (ten Brink et al., 2023). That work explains ecological conditions favoring mixed germination; the present extension instead establishes how returns from distinct reproductive mechanisms can be compared on a common accounting basis. Moreover, this extension also accounts for unequal production costs and delays before reproduction (Dorken et al., 2025), as well as genetic transmission through different reproductive routes (see: Lloyd, 1976; Xu, 2024). Once these contributions have been calibrated, I ask which portfolio composition minimizes variance at a specified expected fitness and which composition maximizes long-run return. I then develop a general model that can be applied to any set of identifiable reproductive outputs that draw on a common budget and have comparable returns, and provide an analytic demonstration using a hypothetical organism (a plant) that produces two seed morphs and a clonal propagule.

Three measurement problems must be resolved to effectively compare heteromorphic offspring portfolios. First, direct comparisons of offspring counts is obviously insufficient: their investments require a common resource scale (Goldberg et al., 2020; Dorken et al., 2025), and their fitness contributions generally require a common temporal and demographic reference framework (Caswell, 2001). Second, fitness returns must be recorded across common or similar environmental states to produce useful measures of covariance. Third, the minimum variance at a prescribed mean and the maximum rate of multiplicative growth (i.e., intrinsic rate of increase) are distinct objectives, and allocation predictions to maximize each must be calculated separately.

112 In this paper, I provide a portfolio approach to address these challenges. I first establish a
113 framework by defining comparable investment and fitness returns across reproductive
114 mechanisms, and then derive calculable minimum-variance and maximum log-growth
115 equations to test predictions. I then use a four-environment hypothetical example to show
116 how adding a clonal offspring can alter the attainable risk, long-run growth, and reproductive
117 investment profiles for existing seed morphs. In doing so, I integrate existing portfolio
118 optimization frameworks (see: Markowitz, 1952; Kelly, 1956; Hakansson, 1971; Cover and
119 Thomas, 2006) to generate something new: an explicit cross-mechanism of reproductive
120 accounting and a set of tools to describe the measurable consequences of differences in
121 morph-specific allocation.

THEORETICAL FRAMEWORK

Biological accounting and model assumptions

To compare distinct reproductive outputs, we must first define what scarce resource is invested and what is deemed to count as a reproductive return. Consider an organism producing two seed morphs and a clonal propagule. Output counts alone cannot reveal fitness consequences: a seed may fail before establishment, while a ramet may persist and reproduce later. Prior work has shown that reproductive costs can reflect some combination of costs associated with current investment, subsequent survival, and future reproductive success (Obeso, 2002; Dorken et al., 2025). Consequently, in this analysis we define an output by its production route and credit its attributable contribution to later reproduction. We also do not treat distinct reproductive outputs as demographically interchangeable.

We begin with a fixed reproductive budget over a defined production interval, as has been implemented in classical resource-allocation models (Smith and Fretwell, 1974; Roff, 1992; Stearns, 1992). The limiting resource might be biomass, energy, or carbon, but every output must be charged in the same units. A return per unit investment equals the fitness contribution attributable to an output divided by its production cost. This separates reproductive investment from propagule number. Given these definitions, allocation accounts for establishment, survival, later reproduction, and consequences for parental fitness under one consistent convention (Obeso, 2002; Goldberg et al., 2020). Next, the fitness currency must identify a genetic or demographic target and a shared reference census. For example, a dormant seed and an established ramet may contribute to an individual's lifetime fitness at different times. Here, I compare them at a specific time point and/or express later contributions in common reproductive-value units (Fisher, 1930; Caswell, 2001; Tuljapurkar, 1990). Genetic transmission requires equally consistent accounting of maternal and paternal

routes (Lloyd, 1976; Xu, 2024). For example, a heterozygous parent transmits a specified allele through an ovule with probability one half. However, when a heterozygous parent self-fertilizes, the seed receives an expected half-copy of the focal allele via the ovule and another half-copy via pollen. Together, these give an expected total of one allele copy per seed, before accounting for establishment (Lloyd, 1976). This is not the same as the probability that the seed carries the allele at all, which is three-quarters (Crow and Kimura, 1970). A clonal ramet, by comparison, inherits one copy of the focal allele, assuming no somatic mutation (Harper, 1977; Schoen and Schultz, 2019). To compare these reproductive routes fairly, we must account for the resources invested in pollen whenever we count its genetic contribution. We must also avoid counting establishment or future reproductive benefits more than once. For connected ramets, this means determining to what degree the ramet adds to the reproductive value of the entire genet, rather than counting the ramet's contribution and then counting the same benefit again as a contribution to its parent (Harper, 1977; Goldberg et al., 2020). Supplementary Section S1 works through these distinctions.

In this paper, our baseline model allocates a fixed budget among n output types. We let each nonnegative allocation fraction be x_i , with all fractions summing to one. An output's return per investment unit is deemed to be fixed within each environmental state, and investment in it (i.e., increasing the number or quality of one reproductive output) does not directly alter the return per unit invested in another output; it only affects the overall tradeoff. Consequently, the total return is additive. Allocation is determined before the environmental state is known rather than in response to an informative cue; this distinguishes the baseline from cue-driven plasticity (Simons, 2011). This formulation seems to reflect natural conditions; for example, in a trimorphic desert annual, moisture, nutrients, and competition alter the proportions and mass allocated to different diaspores (Gan et al., 2020). However, the present model does not

treat cue-dependent changes as a single fixed strategy. Developmental constraints may further restrict feasible mixtures; physiological integration or diminishing returns would require an allocation-dependent, nonlinear extension (Goldberg et al., 2020).

Joint environmental returns and covariance

Rather than simply taking a weighted average of all output fitness, the portfolio outputs must be observed together to establish whether they buffer or reinforce one another's fluctuations (Real, 1980; Frank and Slatkin, 1990; Venable and Brown, 1988). For example, experiments in the clonal grass *Stipa breviflora* found that reproductive and vegetative ramets responded differently to warming and precipitation. Moreover, no sexual–clonal trade-off was observed (Saixiyala et al., 2023). This example illustrates why taking paired measurements of output returns is critical, and it can be incorrect to assume that an environmental factor (in this case, drought) necessarily favours one route. In our theoretical framework, an environmental state therefore represents the complete set of conditions from output production to the common fitness census.

We can then assign each of m environmental states a probability π_e and obtain a return for each output in every state. The return matrix R has environmental states in rows and reproductive outputs in columns; its entry in row e and column i therefore represents the return of output i in environment e . As shown above, empirical tests should use paired observations, since fitness returns from one population and ramet returns from an unrelated second population do not establish their covariance in a common reproductive system.

We can then weight each output's returns by state probabilities to yield a mean. Next, weighting the paired deviations from those means gives their associated variance and

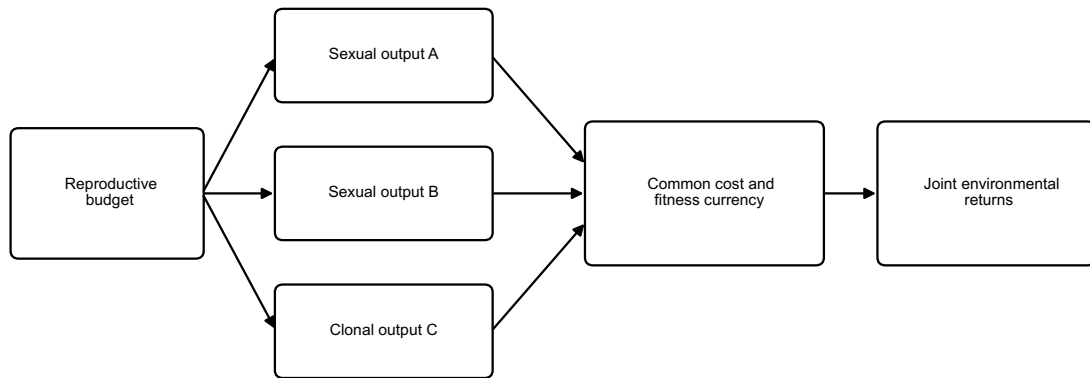
covariance. In this scheme, a negative covariance means that two outputs tend to deviate in opposite directions, whereas a positive covariance means they deviate in the same direction (Frank and Slatkin, 1990; Starrfelt and Kokko, 2012). The effect of each output depends on its covariance with the existing portfolio, and not merely on whether its covariance with any one component is negative or not.

Minimum variance at fixed fitness and maximum long-run growth

We can then use these returns to address two biological objectives. At a specified expected return, we can first identify the feasible allocation with the smallest variance; this involves fixing the mean to prevent a uniformly unproductive strategy from appearing successful merely because it generates very consistent returns. Repeating this calculation across attainable means gives a minimum-variance locus, extending the risk-allocation treatment of Hughes (2018) and related diversification models (Real, 1980; Venable and Brown, 1988; Yasui, 2022). Subsequently, we can maximize expected log growth when reproductive returns cause a tracked lineage to grow exponentially across generations (Lewontin and Cohen, 1969; Kelly, 1956). In this case, the fitness return credited to the reproductive budget should be calibrated using a positive per-generation multiplication factor. Adult carryover must either be included once in that factor or be absent over the chosen interval, since dropping an additive survival contribution can change the optimum (Caswell, 2001; Tuljapurkar, 1990). Moreover, I note that it is well known that a propagule count or allele-copy count is not automatically evidence of a lineage growth multiplier.

In what follows we derive objectives and an output-inclusion criterion; the illustrative model subsequently applies them to four hypothetical environments.

221 With investment and returns defined on a common scale, we can now derive whole-portfolio
222 performance, the least-variable allocations at fixed fitness, and the separate condition for
223 improving long-run growth. Figure 1 summarizes the accounting steps.
224



227 **Figure 1.** A hypothetical reproductive portfolio comprising three heteromorphic reproductive
 228 outputs. Outputs produced through different mechanisms draw on the same reproductive
 229 budget. Their returns are expressed on a common cost and fitness scale, and joint
 230 performance is calculated from the joint environmental performance of the complete strategy.
 231

232 *Constructing the reproductive portfolio*

233 We begin by calculating the return of the whole organism rather than considering each
 234 propagule in isolation. For any given environment, we expect that a fraction x_i of the
 235 reproductive budget is assigned to output i . Each unit of that investment generates return r_i in
 236 that environment. Multiplying the allocation by its return gives that output's contribution to
 237 the strategy, and the sum of all such contributions is equivalent to the return of the complete
 238 portfolio.

$$239 \quad W_e(\mathbf{x}) = \sum_{i=1}^n x_i r_i(e) = (\mathbf{R}\mathbf{x})_e \quad (1)$$

240

241 Equation (1) shows a portfolio's return for a given environment. To compare strategies before
 242 the environment is known, we can next calculate their expected returns. For any number of
 243 environmental configurations, each environmental outcome has probability π_e . We can
 244 therefore multiply equation (1) by that probability and add over all states. Because the
 245 allocation is fixed before the state occurs, we can collect the terms belonging to each output
 246 and replace its probability-weighted return by its mean, μ_i as follows:

247

$$248 \quad E[W(\mathbf{x}, E)] = \sum_e \pi_e \sum_i x_i r_i(e) = \sum_i x_i \mu_i = \mathbf{x}^T \boldsymbol{\mu} \quad (2)$$

249

250 This result gives the portfolio's expected mean return. It does not yet tell us how uncertain
 251 that return is. To calculate risk, we first find how far the whole-portfolio return departs from
 252 its mean in each environment. Subtracting equation (2) from equation (1) leaves the
 253 allocation-weighted deviations of the separate outputs. We square the total deviation,
 254 multiply by the probability of the relevant environment, and add over states as follows:

255

$$256 \quad \text{Var}[W] = \sum_e \pi_e \sum_i \sum_j x_i x_j [r_i(e) - \mu_i][r_j(e) - \mu_j] \quad (3)$$

Expanding the squared sum in equation (3) produces a term for every pair of outputs. The probability-weighted product of two outputs' deviations is their covariance. Denote the matrix of those covariances by Σ . Grouping the terms by output therefore gives:

$$\text{Var}[W] = \sum_i \sum_j x_i \Sigma_{ij} x_j = \mathbf{x}^T \Sigma \mathbf{x} \quad (4)$$

Equation (4) represents the portfolio variance. For two outputs it reduces to the variance calculation reported in Hughes (2018) for two seed morphs, and this can be generalized to any organism producing two morphs in the same way. However, for a portfolio containing three outputs (for example, two seed morphs and one stolon), the portfolio analysis must include the covariance between each seed morph and the clonal output, as well as covariance between the two seeds. Thus, measurements of the cross-mechanism covariances are required to determine whether different reproductive routes buffer one another. Once Equation (4) is computed, we will have converted a set of biologically different outputs into a comparable expected return and a comparable risk for the combined output portfolio.

Finding the minimum-variance frontier

Theoretically, a consistently unproductive output could have low variance without providing a useful reproductive strategy. A fixed-mean comparison separates a risk benefit from an apparent reduction in risk caused simply by lowering expected fitness (Real, 1980; Hughes, 2018). At a target mean M , we therefore minimize variance over the feasible allocations as follows:

$$V_n(M) = \min_{\mathbf{x}} \mathbf{x}^T \Sigma \mathbf{x}, \quad \mathbf{x} \in \mathcal{A}, \quad \mu^T \mathbf{x} = M \quad (5)$$

282

283 In equation (5), the feasible set contains allocations permitted by the budget and any
284 developmental restrictions. Using this equation we can solve for each attainable value of
285 expected fitness. The resulting solutions form the minimum-variance point: at a given mean,
286 no feasible allocation lies below it. The portion on which variance cannot be reduced and
287 mean cannot be increased simultaneously is the efficient frontier in the stricter mean–
288 variance sense. We use the full minimum-variance locus because it displays the trade-offs
289 over all biologically attainable means.

290

291 Next, we can ask how access to another reproductive output can change this frontier. For
292 example, suppose an organism already allocating reproductive effort among n outputs instead
293 allocates to $n + 1$. The first trivial case is where the new output receives zero investment,
294 requires no obligatory expenditure merely to remain available, and leaves the original options
295 unchanged. The organism can therefore reproduce every old portfolio by investing nothing in
296 the new output. It can also try additional allocations that were unavailable before. Minimizing
297 variance over this larger set gives:

298

299
$$V_{n+1}(M) \leq V_n(M) \quad (6)$$

300

301 This result expresses the opportunity created by an additional output: at any mean that the
302 original strategy could attain, the best available variance cannot become greater simply
303 because more allocations are possible. To determine the size of the improvement, we subtract
304 the minimum variance of the enlarged portfolio from that of the original one:

305

306
$$\Delta V(M) = V_n(M) - V_{n+1}(M) \geq 0 \quad (7)$$

Here, any positive value of ΔV shows that the additional output creates a lower-risk strategy at that expected return. Moreover, a value of zero means that the available allocation set does not improve the frontier there. In addition, the costs of developing or maintaining an additional reproductive mechanism must be included in the resource budget before this comparison can be made, which leads us to then consider which nonzero allocations an organism can actually choose.

How covariance determines the contribution of a new output form

We can see how diversification works by considering one additional output at a time. Let P be the return of an existing reproductive portfolio and C the return of a candidate output, such as a stolon. Suppose the organism transfers a small fraction t of its investment from P to C without changing the relative proportions of the original outputs. The new return would therefore be:

$$W(t) = (1 - t)P + tC, \quad 0 \leq t \leq 1 \quad (8)$$

To calculate the variance of this quantity, we square the weighted deviations of P and C from their means. The squared contribution of P is its variance, v , multiplied by the square of its remaining allocation. The corresponding contribution of C is its variance, s , multiplied by the square of t . The resulting cross-product gives twice the covariance, c , which is then multiplied by both allocation fractions:

$$V(t) = (1 - t)^2v + t^2s + 2t(1 - t)c \quad (9)$$

With Equation (9) we can now ask whether the first small real investment in C reduces the variance of the existing portfolio. Expanding equation (9) gives $v + 2t(c - v) + t^2(v + s - 2c)$. We can then take its derivative with respect to t and evaluate it at $t = 0$. The result is $2(c - v)$. This means that a small introduction of C decreases variance when its covariance with P is less than the variance of P itself. The initial benefit depends on how the new output performs alongside the whole existing portfolio and its variance determines how that benefit changes as its allocation increases.

There is one further distinction in this calculation. If C has a different mean from P , shifting investment between them likely also changes the mean value or return of the output portfolio. The covariance condition therefore establishes a marginal reduction in variance, whereas equation (5) answers the stricter question of how variance can be reduced when expected fitness remains unchanged. We use the latter comparison in our analytical test below.

From minimum risk to evolutionary fitness

Minimum variance at a fixed mean does not by itself identify which allocation pattern is favored under multiplicative lineage growth. For example, if a lineage increases by a positive factor W each generation, its abundance over successive generations depends on the product of those factors. Taking logarithms turns that product into a sum, whose long-run average is expected log growth under stable environmental frequencies (Lewontin and Cohen, 1969; Kelly, 1956). Other work has considered a separate measure combining the mean and variability of log growth rather than equating minimum variance with maximum growth (Okabe and Yoshimura, 2022). We therefore use the distinct objective:

$$\max_{\mathbf{x} \in \mathcal{A}} g(\mathbf{x}) = \mathbb{E}[\log(\sum_i x_i R_i)] \quad (10)$$

Unlike equation (5), equation (10) does not resolve or fix the arithmetic mean, but both objectives nonetheless use the same calibrated return distribution. We assume positive scalar lineage multipliers and environmental frequencies for which time-averaged log growth converges to its expectation; age-structured or otherwise non-scalar systems require a different growth analysis (see: Caswell, 2001; Tuljapurkar, 1990).

We can now determine whether any individual output type merits investment in the complete strategy. Increasing the allocation x_i changes the total return by R_i for each unit added, before the budget is rebalanced. Taking the derivative of the logarithm multiplies this change by $1/W$. Averaging over environments therefore gives the marginal contribution:

$$\frac{\partial g}{\partial x_i} = E \left[\frac{R_i}{W(x,E)} \right] \quad (11)$$

At maximum fitness (e.g., the optimum), the returns on outputs receiving investment must balance once the common budget is considered. We can then introduce a multiplier λ to require that all allocations sum to one. That is, for every output with positive allocation, the derivative shown in equation (11) equals λ . If this is true, we can then multiply each equality by that output's allocation and add them. The numerator becomes the complete portfolio return W , and the sum on the left is $E[W/W]$, or one. Because the allocations also sum to one, the right side equals λ . Hence $\lambda = 1$. Outputs in use meet this threshold and any unused output cannot exceed it at the optimum:

$$E \left[\frac{R_i}{W^*} \right] = 1 \text{ if } x_i^* > 0; \quad E \left[\frac{R_i}{W^*} \right] \leq 1 \text{ if } x_i^* = 0 \quad (12)$$

This provides a direct biological test for an evolutionary scenario in which an output may be or may have evolved. We can let P be the currently optimized portfolio and C a candidate output. We transfer a small fraction of investment from P to C , as in equation (8), but now calculate the change in expected log growth. Differentiating $\log[(1 - t)P + tC]$ with respect to t and evaluating at zero gives $E[(C - P)/P]$. Since $E[P/P] = 1$, a small investment in C improves long-run growth precisely when:

$$E\left[\frac{C}{P}\right] > 1 \quad (13)$$

Equation (13) gives the marginal inclusion condition in a measurable form: compare the candidate output with the whole portfolio it would join in each shared environmental state, then average the ratios. Importantly, any biologically evolvable output can improve growth despite a lower standalone return if it is capable of contributing disproportionately where the original portfolio performs poorly. This criterion itself is established in log-optimal portfolio theory (Kelly, 1956; Cover and Thomas, 2006), and in our framework its role is to evaluate reproductive outputs that differ in mechanism.

ILLUSTRATIVE MODEL

This framework can be useful for identifying the adaptive dynamics at play when morph distributions differ across time and space among populations or clades. To illustrate this, we can specify a hypothetical organism with sexual seed morphs A and B and clonal output C. We can then suppose four equally probable environmental states that determine the cost-adjusted returns (fitness) of each morph. This construction allows two comparisons using a common dataset: one that identifies the minimum variance at a fixed arithmetic mean and another that identifies unconstrained long-run growth optima.

Four-state reproductive return model

We first stipulate the following positive returns per common investment unit and reference census. Let R represent a return matrix. Each row represents one environmental state, and each column gives the reproductive return per unit of investment for seed A, seed B, or clone C. Let also π represent the vector of environmental probabilities. Because the four states are equally likely, each has a probability of 0.25. The superscript T indicates that the probabilities are written as a column vector. Thus:

$$R = \begin{pmatrix} 9 & 1 & 2 \\ 1 & 4 & 2 \\ 2 & 1 & 5 \\ 7 & 2 & 4 \end{pmatrix}, \quad \pi = (0.25, 0.25, 0.25, 0.25)^T \quad (14)$$

We then represent the vector of expected reproductive returns as μ , and each entry gives the mean return per unit of investment for one reproductive output, averaged across the four environmental states. The three outputs then have arithmetic means of 4.75, 2, and 3.25, respectively:

420

$$\mu = \begin{pmatrix} \frac{19}{4} \\ 2 \\ \frac{13}{4} \end{pmatrix} \quad (15)$$

421

Their covariance matrix, calculated from paired state-specific deviations, is:

422

$$\Sigma = \begin{pmatrix} \frac{179}{16} & -\frac{9}{4} & -\frac{15}{16} \\ -\frac{9}{4} & \frac{3}{2} & -\frac{3}{4} \\ -\frac{15}{16} & -\frac{3}{4} & \frac{27}{16} \end{pmatrix} \quad (16)$$

423

The covariance matrix is positive definite, so no nonzero portfolio has constant returns across

424

all four states. The illustration permits risk reduction without assuming a perfectly risk-free

425

allocation. Supplementary Section S2 gives the complete calculation.

426

427

428 RESULTS

429 *Reduction in variance at unchanged expected fitness*

430 At a common expected return M , the seed-only and expanded systems have different
 431 attainable minimum variances. Restricting investment to A and B yields:

432

$$433 \quad V_2(M) = \frac{50M^2 - 260M + 353}{22}, \quad 2 \leq M \leq \frac{19}{4} \quad (17)$$

434

435 Allowing clone investment t while maintaining the same mean gives the feasible allocation:

436

$$437 \quad \mathbf{x}(M, t) = \begin{pmatrix} \frac{4M - 5t - 8}{11} \\ \frac{19 - 4M - 6t}{11} \\ t \end{pmatrix} \quad (18)$$

438

439 Nonnegative investment limits the clone fraction to the smaller of $(4M - 8)/5$ and $(19 -$
 440 $4M)/6$, with a lower bound of zero. Substitution into the common return matrix yields:

441 Next we substitute the allocations in equation (18) into the four environmental returns of
 442 equation (14). For each state we subtract the common mean M , square the deviation, then

443 average the four squared values. After collecting the terms in M and the remaining allocation
 444 t , the variance is then represented as:

445

$$446 \quad V_3(M, t) = \frac{50M^2 - 68Mt - 260M + 110t^2 + 112t + 353}{22} \quad (19)$$

447

448 Minimizing this quadratic over the feasible interval gives:

449

$$450 \quad t^*(M) = \max \left\{ 0, \min \left[\frac{17M - 28}{55}, \frac{4M - 8}{5}, \frac{19 - 4M}{6} \right] \right\} \quad (20)$$

Equation (20) therefore gives the optimal fraction of reproductive investment allocated to clone C at any specified expected return M . The first term gives the unconstrained minimum of the variance function, while the remaining terms impose the investment limits: no output can receive a negative allocation, and the total allocation must sum to one. These constraints determine which reproductive outputs are included in the minimum-variance portfolio. At low expected returns (i.e., up to $M = 20/9$), the optimal strategy uses seed B and clone C, with no investment in seed A. However, between $M = 20/9$ and $M = 1213/322$, all three outputs receive investment, and above $M = 1213/322$, the optimum uses seed A and clone C, with no investment in seed B. These thresholds occur where the unconstrained optimum reaches an allocation boundary and one of the seed fractions becomes zero. They are therefore changes in portfolio composition, and do not necessarily require any additional assumptions about the organism itself.

Furthermore, since the expanded reproductive system can always reproduce any seed-only allocation by assigning zero investment to the clone, its minimum variance cannot exceed that of the seed-only system at the same expected return. For this particular return matrix, adding the clone reduces minimum variance at every expected return strictly between 2 and 4.75. At these two endpoints, the mean-return constraint permits only investment entirely in B or entirely in A, respectively, so the two minimum-variance curves meet. Figure 2 shows the complete comparison and highlights the reduction in variance at an expected return of three. Supplementary Section S2 provides the algebra and the complete piecewise minimum-variance locus.

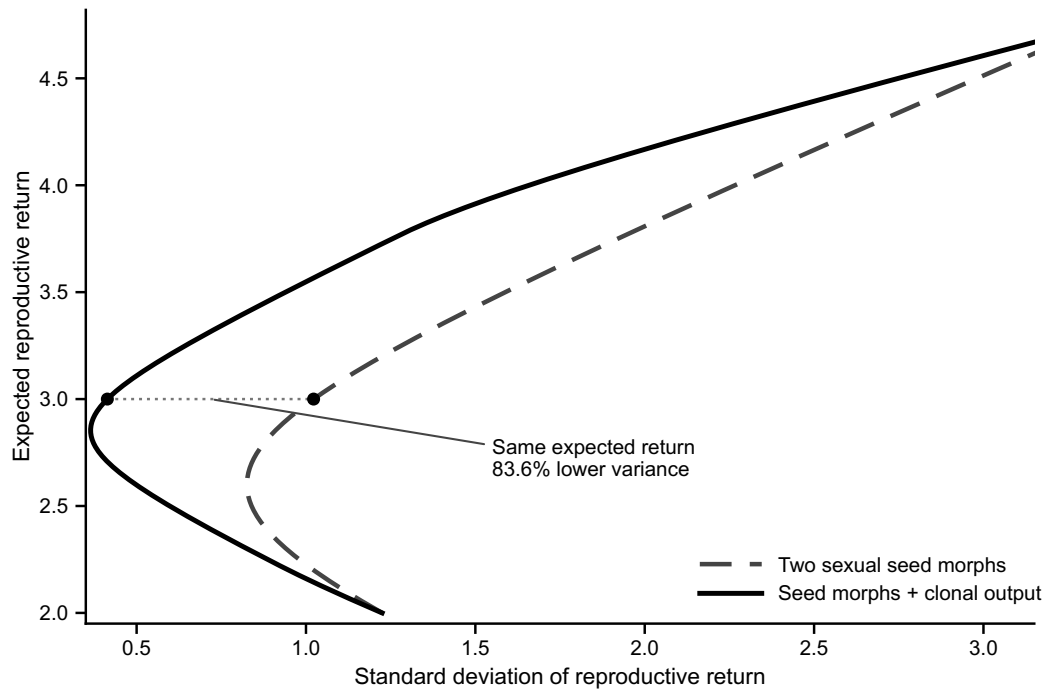


Figure 2. Minimum-variance loci for seed morphs A and B and the same system with an optional clone C across four equiprobable hypothetical environments. At expected return three, adding the clone lowers minimum variance by 83.6%. The horizontal axis shows standard deviation, not variance.

At this mean, the seed-only strategy has a minimum variance of 1.045, compared with 0.171 when C is available; this represents a reduction of 83.6% without changing expected fitness. The respective allocations are 36.4% A and 63.6% B for the seed-only strategy, and 174% A, 40.8% B, and 41.8% C for the expanded strategy. The expanded portfolio still varies across environmental states and is not risk-free.

Higher long-run growth after adding a clonal output

When we optimize the seed-only strategy for expected log growth, its optimum allocates investment between A and B as follows (full calculation in Supplementary Section S3):

$$\mathbf{x}_{AB}^* = \begin{pmatrix} 0.89485 \\ 0.10515 \\ 0 \end{pmatrix} \quad (21)$$

Here, the seed-only optimum has geometric mean return 3.387. Clone C performs less well on its own (geometric mean 2.991), but its expected return relative to the seed portfolio is 1.256, above the inclusion threshold of one in equation (13). It can therefore improve long-run growth when introduced at the margin.

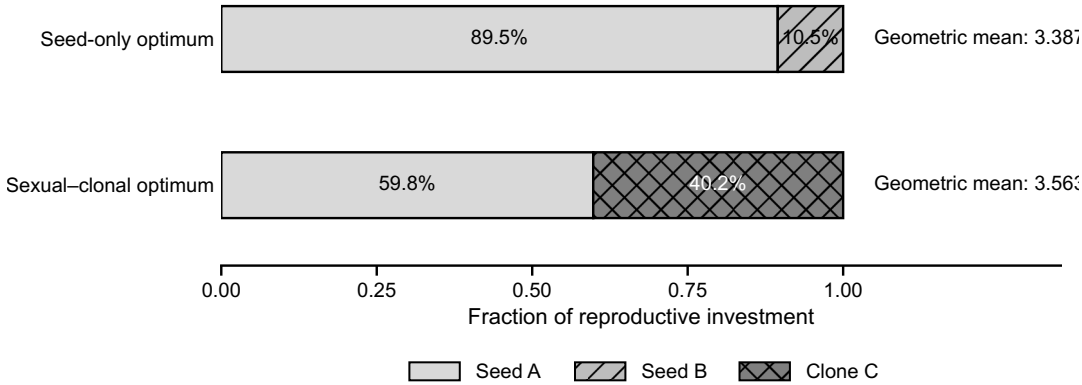
Reoptimizing after allowing C removes B from the optimal allocation. The full optimum can be represented as:

$$\mathbf{x}_{ABC}^* = \begin{pmatrix} 0.59812 \\ 0 \\ 0.40188 \end{pmatrix} \quad (22)$$

This new portfolio increases geometric mean growth from 3.387 to 3.563 (5.2%), although its arithmetic mean falls from 4.461 to 4.147. At those independently optimized allocations,

504 variance falls from 8.552 to 3.824; those variances are not a fixed-mean comparison. At the
505 expanded optimum's own mean, the seed-only minimum variance is 6.122, compared with
506 3.824 when C is available, a fixed-mean reduction of 37.5%. Figure 3 shows the growth-
507 optimal allocations; Supplementary Section S3 documents the optimization.
508

509



510

511 **Figure 3.** Independently optimized seed-only and sexual-clonal allocations in the
512 hypothetical four-state model. Adding the clone raises geometric mean return from 3.387 to
513 3.563. The lower arithmetic mean and lower variance reported in the text concern
514 independently optimized strategies with different means.
515

516

517 *Adding the clone alters reproductive investment in the original seed outputs*

518 In this example, the possibility of reproduction via the clone changes the theoretical best
519 strategy for the original seed morphs even though their own environmental returns do not
520 change. With only A and B available, the organism invests 10.5% in B. However, after C
521 becomes available, the optimal portfolio uses A and C and does not invest in output B. Thus,
522 in this new portfolio, B's expected relative contribution is only 0.918, a value that is below
523 the inclusion threshold of one. In such a case B has not lost its reproductive capacity, but it
524 has become less useful relative to the alternative outputs now available. This example
525 therefore illustrates the general point that output fitness relative to alternatives can dominate
526 absolute fitness in the environment.

527

DISCUSSION

Reproductive outputs acquire value through their combinations

The framework addresses a practical problem in life-history analysis: offspring counts cannot compare reproductive routes with different costs, delays, genetic transmission, and contributions to future fitness. Classical allocation theory relates offspring number and size to finite parental resources (Smith and Fretwell, 1974; Roff, 1992; Stearns, 1992), while recent work emphasizes how plant reproductive costs are measured and attributed (Dorken et al., 2025). I extend that accounting to a portfolio of unlike outputs. Once their returns are expressed per unit investment at a common census and measured under shared environments, their covariances and attainable allocations can be evaluated together.

Our analytical result illustrates portfolio complementarity: the clone contributes most where the seed-only strategy performs relatively poorly, lowering variance at a fixed mean and improving long-run growth under a different, multiplicative objective. The clone need not outperform the existing seed portfolio in isolation. Adding it also removes B from the growth-optimal mixture despite leaving B's own returns unchanged. The two comparisons should not be conflated: minimum variance at a specified mean measures the diversification opportunity, whereas expected log growth selects an allocation under the stated demographic assumptions (Lewontin and Cohen, 1969; Starrfelt and Kokko, 2012; Yasui, 2022).

Taken together, our results connect reproductive allocation to a wider literature on diversification under uncertainty (Scholl et al., 2020; Abley et al., 2024). For example, Venable and Brown (1988) modeled the interacting effects of dormancy, dispersal, and seed size; Frank and Slatkin (1990) clarified components of reproductive variance; and Starrfelt and Kokko (2012) emphasized the joint importance of means, variances, and correlations.

Reviews of clonal plant mating describe interactions between sexual and vegetative routes (Vallejo-Marín et al., 2010; Barrett, 2015). Orive et al. (2023) explored evolutionary consequences of partial clonality, while Weissman et al. (2025) showed that stochastic population outcomes can differ from deterministic geometric-mean predictions. Those demographic questions remain distinct from the fixed-budget, additive allocation calculation developed here.

This paper is designed to build on existing theory. An earlier paper supplied a fixed-mean minimum-risk benchmark for allocating investment among seed morphs (Hughes, 2018). In an analytical model and evolutionary simulations, ten Brink et al. (2023) subsequently examined early- versus late-germinating seeds in perennials, showing how false starts to a growing season, competitive advantages during recruitment, and adult survival jointly affect whether mixed germination strategies evolve. That work identifies ecological mechanisms that favor diversification within seed reproduction. The present model asks a complementary question: once unlike outputs have been measured in a common investment and lineage-fitness currency, what do their joint environmental returns imply for the minimum-variance frontier and for long-run growth? We note that neither analysis makes competition, plasticity, or age structure irrelevant. If these processes cause output returns to depend on allocation or population state, the additive portfolio becomes an informative benchmark rather than a complete evolutionary model.

Biological systems for comparative analysis

Plants provide several routes for direct comparison. Chasmogamous and cleistogamous flowers differ in mating circumstances and costs (Schoen and Lloyd, 1984; Culley and Klooster, 2007). Furthermore, in the stoloniferous plant *Viola odorata*, those sexual routes

could also be compared with vegetative propagation. Floral developmental differences are well-documented, but an optimized three-output portfolio would require measurement of paired costs and subsequent returns in the same environments (Mayers and Lord, 1983). To date such information has not yet been measured. Evidence from perennials also shows why the relevant outputs must be measured rather than inferred from their appearance. Santos-Gally et al. (2020) found two fruit morphs within the capitula of the perennial shrub *Tithonia diversifolia*; morph ratios differed among populations, and the direction of the difference in germination success between morphs depended on the population. These observations identify candidate outputs and environmental variation, but population-level contrasts do not supply the paired, cost-adjusted returns of one reproductive portfolio. In the perennial grass *Danthonia compressa*, Cheplick (2023) documented spatial and temporal variation in chasmogamous and cleistogamous reproduction. The study identifies variation relevant to seed-route comparisons; a clonal component must be independently established before a three-output model can be fitted. For greater duckweed, *Spirodela polyrhiza*, daughter fronds and dormant turions provide immediate versus delayed vegetative outputs. Mejbél and Simons (2018) investigated how birth order produces differences in turion phenology among clonally related offspring, while Kuehdorf et al. (2014) investigated turion production. Flowering and seed production occur in duckweeds, but a measured frond–turion–seed portfolio for the same population cannot simply be inferred from their presence (Fourounjian et al., 2021).

Other studies of seed systems provide increasingly concrete pieces of the required measurement programme. For example, Chen and Giladi (2020) linked variation in dispersive-diaspore morphology within *Geropogon hybridus* to terminal velocity and seedling emergence; their measurements establish relationships among traits and early

performance, not a comparison of complete returns across its reproductive routes. In another paper, Gan et al. (2020) experimentally varied moisture, nutrient availability, and density in *Ceratocarpus arenarius*. They found that the production and proportional investment of its three diaspore morphs changed in response to specific treatment. In trimorphic *Atriplex aucheri*, Shoukat et al. (2026) measured production of three seed types across four water-supply treatments: type A production peaked at intermediate water, type B was comparatively stable, and allocation to type C declined with increasing water. Importantly, these experiments approach the model from the production side; they do not measure the later fitness of every output at a shared census. Wang et al. (2020) additionally documented three diaspore types of *Atriplex centralasiatica* with differing dispersal, dormancy, and seed-bank behavior, identifying distinct routes whose full returns could be followed across environmental histories.

The relevant environment can also extend beyond the conditions experienced by the parent or the first census. Gan et al. (2023) showed that parental drought and seed-morph identity interact in *Synedrella nodiflora*, with different transgenerational consequences for offspring drought tolerance. Van Den Elzen and Emery (2026) found that three closely related *Lasthenia* species altered both mean germination timing and its within-season variability under contrasting moisture regimes; the magnitude of temporal diversification itself was environmentally responsive. The first finding motivates tracking maternal history when defining a shared environmental state, and the second shows why an empirical test must distinguish diversified output production from plastic adjustment to a cue. Although linked to the underlying logic of output diversification, neither study by itself demonstrates selection for the fixed-allocation optimum derived here.

Examples exist outside the plant kingdom as well, although fewer animal systems produce many distinct morphs. One example is the freshwater cnidarian *Hydra oligactis*, which produces both asexual buds and multiple types of sexually derived resting eggs that differ in production conditions and their resistance to winter stress. Experiments have documented nuanced trade-offs involving stem cells and regeneration and may involve temperature-dependence (Sebestyén et al., 2018). Temperature-dependent alternation between budding and gamete formation also illustrates why pre-environment fixed allocation must be distinguished from cue-driven plasticity (Littlefield et al., 1991; Simons, 2011). Cyclically parthenogenetic *Daphnia* provide another non-plant system: females produce immediately developing asexual offspring, while sexual reproduction entails production of males and fertilized resting eggs that survive unfavorable periods (Ebert, 2022). Field observations of *D. magna* have shown that sexual investment increases when the opportunity cost of foregoing asexual reproduction falls, although a complete resource-cost comparison of all outputs remains unavailable (Gerber et al., 2018). Rotifers such as *Brachionus plicatilis* likewise produce rapidly developing parthenogenetic offspring and sexually derived dormant eggs; recent studies connect diapause traits with environmental unpredictability and show that cue responses and bet hedging can coexist (Solano-Udina et al., 2025, 2026). In these cyclical systems, male production is a distinct investment route rather than automatically a third independent fitness return: male and resting-egg contributions must be credited without double counting. Although environmentally-induced allocation differences do not represent a test of our pre-environment fixed-allocation model, such systems may be fertile ground for portfolio analysis when data describing a cost-adjusted, joint return matrix is available.

Empirical predictions

Testing the model derived here requires measuring all available reproductive outputs, the resources invested in each (Goldberg et al., 2020), and their contributions to fitness at a common reference census (Caswell, 2001). Moreover, these measurements must be made across the same environmental conditions so that the relative performance of the different outputs, and their covariance, can be determined (Starrfelt and Kokko, 2012). The empirical studies discussed above report much of the necessary groundwork, including fitness measures characterizing the production of different outputs, differences in output performance, and output-specific responses to environmental variation. The next step would be to bring these measurements together by designing an empirical system that would record both the cost and subsequent fitness contribution of every output.

With these data, we can construct the return matrix and calculate the allocation that minimizes variance at any specified mean fitness. We can then compare these predictions with observed reproductive allocations to test whether organisms approach the predicted minimum-risk strategies. The model also makes a separate prediction about long-run growth: an additional output should enter the optimal portfolio when its expected return relative to the existing portfolio exceeds one. We can test this prediction by measuring whether reallocating investment to the additional output increases geometric mean fitness across environmental conditions. Overall, the value of the framework developed in this paper is that comparisons among outputs can allow us to distinguish reproductive diversification from the mere production of different offspring types. However, such tests should also account for environmentally induced plasticity, developmental constraints, diminishing returns on investment, and demographic stochasticity, all of which can influence reproductive allocation

and its fitness consequences (Caswell, 2001; Weissman et al., 2025; Solano-Udina et al., 2026).

Scope and limitations of the portfolio model

The model describes fixed-budget, additive portfolios with returns determined before the environment is realized. Outputs may interact through physiological integration, altered parental survival, or diminishing returns as investment increases (Goldberg et al., 2020); such systems require an allocation-dependent return function rather than the linear baseline. A demographic system in which annual reproductive contributions cannot be represented by a single positive lineage multiplier requires a different long-run fitness calculation (Caswell, 2001; Tuljapurkar, 1990). Finally, we note that demographic stochasticity and finite population size can alter the relevant selection outcome (Gillespie, 1974; Weissman et al., 2025). Thus, all long-run interpretations using this framework must therefore be evaluated against the demographic question being asked.

CONCLUSION

In this paper I use portfolio theory to develop a common accounting framework for reproductive outputs that differ in morphology, timing, or mechanism. Defining cost-adjusted fitness returns at the same census makes it possible to measure their joint environmental performance, calculate the minimum-variance locus, and ask whether another output increases long-run growth. In the hypothetical example, a clone lowers variance at unchanged expected fitness and improves geometric mean growth when the expanded portfolio is independently optimized. Its entry also changes which existing seed morph receives investment: a reproductive output's contribution is conditional on the alternatives available.

The empirical challenge is to measure comparable costs, paired returns, and feasible allocations in systems with sexual, clonal, or temporally differentiated reproduction. This connects established theories of life-history trade-offs, diversified offspring traits, and stochastic fitness with testable cross-mechanism comparisons (Stearns, 1992; Venable and Brown, 1988; Starrfelt and Kokko, 2012; Yasui, 2022). Recent analyses of perennial germination and morph-specific responses to environmental treatments make this programme concrete (ten Brink et al., 2023; Gan et al., 2020; Shoukat et al., 2026), but they cannot substitute for paired lineage-fitness returns. Such data will establish when the portfolio opportunity demonstrated here is realized in nature.

REFERENCES

- Abley, K., Goswami, R., and Locke, J. C. W. (2024). Bet-hedging and variability in plant development: seed germination and beyond. *Philosophical Transactions of the Royal Society B* 379, 20230048. <https://doi.org/10.1098/rstb.2023.0048>
- Barrett, S. C. H. (2015). Influences of clonality on plant sexual reproduction. *Proceedings of the National Academy of Sciences USA* 112, 8859–8866. <https://doi.org/10.1073/pnas.1501712112>
- Baskin, C. C., and Baskin, J. M. (2014). *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd ed. Academic Press, San Diego.
- Bonte, D., Van Dyck, H., Bullock, J. M., et al. (2012). Costs of dispersal. *Biological Reviews* 87, 290–312. <https://doi.org/10.1111/j.1469-185X.2011.00201.x>
- Caswell, H. (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd ed. Sinauer Associates, Sunderland, MA.
- Chen, S.-C., and Giladi, I. (2020). Variation in morphological traits affects dispersal and seedling emergence in dispersive diaspores of *Geropogon hybridus*. *American Journal of Botany* 107, 436–444. <https://doi.org/10.1002/ajb2.1430>
- Cheplick, G. P. (2023). Spatiotemporal variation of chasmogamy and cleistogamy in a native perennial grass: fecundity, reproductive allocation and allometry. *AoB PLANTS* 15, plad020. <https://doi.org/10.1093/aobpla/plad020>

735

736 Childs, D. Z., Metcalf, C. J. E., and Rees, M. (2010). Evolutionary bet-hedging in the real
 737 world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal*
 738 *Society B* 277, 3055–3064. <https://doi.org/10.1098/rspb.2010.0707>

739

740 Cohen, D. (1966). Optimizing reproduction in a randomly varying environment. *Journal of*
 741 *Theoretical Biology* 12, 119–129. [https://doi.org/10.1016/0022-5193\(66\)90188-3](https://doi.org/10.1016/0022-5193(66)90188-3)

742

743 Cover, T. M., and Thomas, J. A. (2006). *Elements of Information Theory*, 2nd ed. Wiley,
 744 Hoboken, NJ. Chapter 16. <https://doi.org/10.1002/047174882X>

745

746 Crow, J. F., and Kimura, M. (1970). *An Introduction to Population Genetics Theory*. Harper
 747 & Row, New York.

748

749 Culley, T. M., and Klooster, M. R. (2007). The cleistogamous breeding system: a review of
 750 its frequency, evolution, and ecology in angiosperms. *The Botanical Review* 73, 1–30.
 751 [https://doi.org/10.1663/0006-8101\(2007\)73\[1:TCBSAR\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2007)73[1:TCBSAR]2.0.CO;2)

752

753 Dorken, M. E., van Kleunen, M., and Stift, M. (2025). Costs of reproduction in flowering
 754 plants. *New Phytologist* 247, 55–70. <https://doi.org/10.1111/nph.70166>

755

756 Ebert, D. (2022). *Daphnia* as a versatile model system in ecology and evolution. *EvoDevo* 13,
 757 16. <https://doi.org/10.1186/s13227-022-00199-0>

758

759 Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

760

761 Fourounjian, P., Slovin, J., and Messing, J. (2021). Flowering and seed production across the
762 Lemnaceae. *International Journal of Molecular Sciences* 22, 2733.

763 <https://doi.org/10.3390/ijms22052733>

764

765 Frank, S. A., and Slatkin, M. (1990). Evolution in a variable environment. *The American*
766 *Naturalist* 136, 244–260. <https://doi.org/10.1086/285094>

767

768 Gan, L., Lu, J., Baskin, J. M., Baskin, C. C., and Tan, D. (2020). Phenotypic plasticity in
769 diaspore production of an amphi-basicaipic cold desert annual that produces polymorphic
770 diaspores. *Scientific Reports* 10, 11142. <https://doi.org/10.1038/s41598-020-67380-0>

771

772 Gan, Q., Liu, J., Liao, H., and Peng, S. (2023). Dimorphism-dependent transgenerational
773 effects facilitate divergence of drought tolerance in *Synedrella nodiflora*. *Journal of Plant*
774 *Ecology* 16, rtac042. <https://doi.org/10.1093/jpe/rtac042>

775

776 Gerber, N., Kokko, H., Ebert, D., and Booksmythe, I. (2018). *Daphnia* invest in sexual
777 reproduction when its relative costs are reduced. *Proceedings of the Royal Society B* 285,
778 20172176. <https://doi.org/10.1098/rspb.2017.2176>

779

780 Gianella, M., Bradford, K. J., and Guzzon, F. (2021). Ecological, (epi)genetic and
781 physiological aspects of bet-hedging in angiosperms. *Plant Reproduction* 34, 21–36.
782 <https://doi.org/10.1007/s00497-020-00402-z>

783

784 Gillespie, J. H. (1974). Natural selection for within-generation variance in offspring number.
 785 Genetics 76, 601–606. <https://doi.org/10.1093/genetics/76.3.601>
 786

787 Goldberg, D. E., Batzer, E., Elgersma, K., Martina, J., and Klimešová, J. (2020). Allocation
 788 to clonal growth: critical questions and protocols to answer them. Perspectives in Plant
 789 Ecology, Evolution and Systematics 43, 125511. <https://doi.org/10.1016/j.ppees.2020.125511>
 790

791 Haccou, P., and Iwasa, Y. (1995). Optimal mixed strategies in stochastic environments.
 792 Theoretical Population Biology 47, 212–243. <https://doi.org/10.1006/tpbi.1995.1009>
 793

794 Hakansson, N. H. (1971). Capital growth and the mean-variance approach to portfolio
 795 selection. Journal of Financial and Quantitative Analysis 6, 517–557.
 796 <https://doi.org/10.1017/S0022109000021463>
 797

798 Harper, J. L. (1977). Population Biology of Plants. Academic Press, London.
 799

800 Hughes, P. W. (2018). Minimal-risk seed heteromorphism: proportions of seed morphs for
 801 optimal risk-averse heteromorphic strategies. Frontiers in Plant Science 9, 1412.
 802 <https://doi.org/10.3389/fpls.2018.01412>
 803

804 Imbert, E. (2002). Ecological consequences and ontogeny of seed heteromorphism.
 805 Perspectives in Plant Ecology, Evolution and Systematics 5, 13–36.
 806 <https://doi.org/10.1078/1433-8319-00021>
 807

808 Kelly, J. L. (1956). A new interpretation of information rate. Bell System Technical Journal
809 35, 917–926. <https://doi.org/10.1002/j.1538-7305.1956.tb03809.x>
810

811 Koons, D. N., Metcalf, C. J. E., and Tuljapurkar, S. (2008). Evolution of delayed
812 reproduction in uncertain environments: a life-history perspective. The American Naturalist
813 172, 797–805. <https://doi.org/10.1086/592867>
814

815 Kuehdorf, K., Jetschke, G., Ballani, L., and Appenroth, K.-J. (2014). The clonal dependence
816 of turion formation in the duckweed *Spirodela polyrhiza*—an ecogeographical approach.
817 Physiologia Plantarum 150, 46–54. <https://doi.org/10.1111/ppl.12065>
818

819 Lennon, J. T., den Hollander, F., Wilke-Berenguer, M., and Blath, J. (2021). Principles of
820 seed banks and the emergence of complexity from dormancy. Nature Communications 12,
821 4807. <https://doi.org/10.1038/s41467-021-24733-1>
822

823 Lewontin, R. C., and Cohen, D. (1969). On population growth in a randomly varying
824 environment. Proceedings of the National Academy of Sciences USA 62, 1056–1060.
825 <https://doi.org/10.1073/pnas.62.4.1056>
826

827 Littlefield, C. L., Finkemeier, C., and Bode, H. R. (1991). Spermatogenesis in *Hydra*
828 *oligactis*. II. How temperature controls the reciprocity of sexual and asexual reproduction.
829 Developmental Biology 146, 292–300. [https://doi.org/10.1016/0012-1606\(91\)90231-Q](https://doi.org/10.1016/0012-1606(91)90231-Q)
830

831 Lloyd, D. G. (1976). The transmission of genes via pollen and ovules in gynodioecious
 832 angiosperms. *Theoretical Population Biology* 9, 299–316. [https://doi.org/10.1016/0040-](https://doi.org/10.1016/0040-5809(76)90050-2)
 833 [5809\(76\)90050-2](https://doi.org/10.1016/0040-5809(76)90050-2)
 834
 835 Markowitz, H. (1952). Portfolio selection. *The Journal of Finance* 7, 77–91.
 836 <https://doi.org/10.2307/2975974>
 837
 838 Mayers, A. M., and Lord, E. M. (1983). Comparative flower development in the
 839 cleistogamous species *Viola odorata*. I. A growth rate study. *American Journal of Botany* 70,
 840 1548–1555. <https://doi.org/10.1002/j.1537-2197.1983.tb10858.x>
 841
 842 Mejbel, H. S., and Simons, A. M. (2018). Aberrant clones: birth order generates life history
 843 diversity in greater duckweed, *Spirodela polyrhiza*. *Ecology and Evolution* 8, 2021–2031.
 844 <https://doi.org/10.1002/ece3.3822>
 845
 846 Obeso, J. R. (2002). The costs of reproduction in plants. *New Phytologist* 155, 321–348.
 847 <https://doi.org/10.1046/j.1469-8137.2002.00477.x>
 848
 849 Okabe, T., and Yoshimura, J. (2022). A new long-term measure of sustainable growth under
 850 uncertainty. *PNAS Nexus* 1, pgac228. <https://doi.org/10.1093/pnasnexus/pgac228>
 851
 852 Orive, M. E., Barfield, M., and Holt, R. D. (2023). Partial clonality expands the opportunity
 853 for spatial adaptation. *The American Naturalist* 202, 681–698. <https://doi.org/10.1086/726335>
 854

855 Philippi, T., and Seger, J. (1989). Hedging one's evolutionary bets, revisited. Trends in
 856 Ecology & Evolution 4, 41–44. [https://doi.org/10.1016/0169-5347\(89\)90138-9](https://doi.org/10.1016/0169-5347(89)90138-9)
 857
 858 Real, L. A. (1980). Fitness, uncertainty, and the role of diversification in evolution and
 859 behavior. The American Naturalist 115, 623–638. <https://doi.org/10.1086/283588>
 860
 861 Roff, D. A. (1992). The Evolution of Life Histories: Theory and Analysis. Chapman & Hall,
 862 New York.
 863
 864 Saixiyala, Chen, L., Yi, F., Qiu, X., Sun, H., Cao, H., Baoyin, T., Ye, X., and Huang, Z.
 865 (2023). Warming in combination with increased precipitation mediate the sexual and clonal
 866 reproduction in the desert steppe dominant species *Stipa breviflora*. BMC Plant Biology 23,
 867 474. <https://doi.org/10.1186/s12870-023-04439-w>
 868
 869 Santos-Gally, R., Muñoz, M., and Franco, G. (2020). Fruit heteromorphism and germination
 870 success in the perennial shrub *Tithonia diversifolia* (Asteraceae). Flora 271, 151686.
 871 <https://doi.org/10.1016/j.flora.2020.151686>
 872
 873 Schoen, D. J., and Lloyd, D. G. (1984). The selection of cleistogamy and heteromorphic
 874 diaspores. Biological Journal of the Linnean Society 23, 303–322.
 875 <https://doi.org/10.1111/j.1095-8312.1984.tb00147.x>
 876
 877 Schoen, D. J., and Schultz, S. T. (2019). Somatic mutation and evolution in plants. Annual
 878 Review of Ecology, Evolution, and Systematics 50, 49–73. <https://doi.org/10.1146/annurev-ecolsys-110218-024955>
 879

880

881 Scholl, J. P., Calle, L., Miller, N., and Venable, D. L. (2020). Offspring polymorphism and
882 bet hedging: a large-scale, phylogenetic analysis. *Ecology Letters* 23, 1223–1231.

883 <https://doi.org/10.1111/ele.13522>

884

885 Sebestyén, F., Barta, Z., and Tököllyi, J. (2018). Reproductive mode, stem cells and
886 regeneration in a freshwater cnidarian with postreproductive senescence. *Functional Ecology*
887 32, 2497–2508. <https://doi.org/10.1111/1365-2435.13189>

888

889 Seger, J., and Brockmann, H. J. (1987). What is bet-hedging? In: Harvey, P. H., and
890 Partridge, L. (eds), *Oxford Surveys in Evolutionary Biology*, vol. 4. Oxford University Press,
891 Oxford, pp. 182–211.

892

893 Shoukat, M. R., Zhang, Y., Yan, K., Buttar, Z. A., and Jiang, L. (2026). Graded water supply
894 decouples vegetative growth, reproductive investment, and nitrogen balance in trimorphic
895 *Atriplex aucheri*. *BMC Plant Biology*, accepted manuscript. [https://doi.org/10.1186/s12870-](https://doi.org/10.1186/s12870-026-09676-3)
896 [026-09676-3](https://doi.org/10.1186/s12870-026-09676-3)

897

898 Simons, A. M. (2011). Modes of response to environmental change and the elusive empirical
899 evidence for bet hedging. *Proceedings of the Royal Society B* 278, 1601–1609.

900 <https://doi.org/10.1098/rspb.2011.0176>

901

902 Smith, C. C., and Fretwell, S. D. (1974). The optimal balance between size and number of
903 offspring. *The American Naturalist* 108, 499–506. <https://doi.org/10.1086/282929>

904

905 Solano-Udina, C., Carmona, M. J., and García-Roger, E. M. (2026). Adaptive responses to
 906 environmental variability in rotifers: integrating plasticity and bet hedging in dormancy exit.
 907 Ecology 107, e70346. <https://doi.org/10.1002/ecy.70346>
 908

909 Solano-Udina, C., Serra, M., Carmona, M. J., and García-Roger, E. M. (2025). Risk-avoiding
 910 strategies in rotifer diapause-related traits in response to environmental unpredictability.
 911 Freshwater Biology 70, e70093. <https://doi.org/10.1111/fwb.70093>
 912

913 Starrfelt, J., and Kokko, H. (2012). Bet-hedging—a triple trade-off between means, variances
 914 and correlations. Biological Reviews 87, 742–755. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-185X.2012.00225.x)
 915 [185X.2012.00225.x](https://doi.org/10.1111/j.1469-185X.2012.00225.x)
 916

917 Stearns, S. C. (1992). The Evolution of Life Histories. Oxford University Press, Oxford.
 918 <https://doi.org/10.1093/oso/9780198577416.001.0001>
 919

920 ten Brink, H., Gremer, J. R., and Kokko, H. (2020). Optimal germination timing in
 921 unpredictable environments: the importance of dormancy for both among- and within-season
 922 variation. Ecology Letters 23, 620–630. <https://doi.org/10.1111/ele.13461>
 923

924 ten Brink, H., Haaland, T. R., Massol, F., and Opedal, Ø. H. (2023). Seasonality and
 925 competition select for variable germination behavior in perennials. Evolution 77, 1791–1805.
 926 <https://doi.org/10.1093/evolut/qpad089>
 927

928 Tuljapurkar, S. (1990). Population Dynamics in Variable Environments. Springer, Berlin.
 929 <https://doi.org/10.1007/978-3-642-51652-8>

930

931 Vallejo-Marín, M., Dorken, M. E., and Barrett, S. C. H. (2010). The ecological and
932 evolutionary consequences of clonality for plant mating. *Annual Review of Ecology,
933 Evolution, and Systematics* 41, 193–213.
934 <https://doi.org/10.1146/annurev.ecolsys.110308.120258>

935

936 Van Den Elzen, C. L., and Emery, N. C. (2026). Recruitment in variable environments:
937 plasticity and bet hedging in the timing of seed germination in three closely related species.
938 *Annals of Botany* 137, 223–231. <https://doi.org/10.1093/aob/mcaf227>

939

940 Venable, D. L. (1985). The evolutionary ecology of seed heteromorphism. *The American
941 Naturalist* 126, 577–595. <https://doi.org/10.1086/284440>

942

943 Venable, D. L., and Brown, J. S. (1988). The selective interactions of dispersal, dormancy,
944 and seed size as adaptations for reducing risk in variable environments. *The American
945 Naturalist* 131, 360–384. <https://doi.org/10.1086/284795>

946

947

948 Venable, D. L., and Lawlor, L. (1980). Delayed germination and dispersal in desert annuals:
949 escape in space and time. *Oecologia* 46, 272–282. <https://doi.org/10.1007/BF00540137>

950

951 Wang, Z., Baskin, J. M., Baskin, C. C., Yang, X., Liu, G., and Huang, Z. (2020). Dynamics
952 of the diaspore and germination stages of the life history of an annual diaspore-trimorphic
953 species in a temperate salt desert. *Planta* 251, 87. [https://doi.org/10.1007/s00425-020-03380-](https://doi.org/10.1007/s00425-020-03380-8)

954 [8](https://doi.org/10.1007/s00425-020-03380-8)

955

956 Weissman, M., Yin, Z., Raynes, Y., and Weinreich, D. (2025). Beyond the (geometric) mean:
957 stochastic models undermine deterministic predictions of bet hedger evolution. *The American*
958 *Naturalist* 205, 572–589. <https://doi.org/10.1086/735690>

959

960 Xu, K. (2024). Effects of selfing on the evolution of sexual reproduction. *Evolution* 78, 879–
961 893. <https://doi.org/10.1093/evolut/qpae016>

962

963 Yang, Y. Y., and Kim, J. G. (2016). The optimal balance between sexual and asexual
964 reproduction in variable environments: a systematic review. *Journal of Ecology and*
965 *Environment* 40, 12. <https://doi.org/10.1186/s41610-016-0013-0>

966

967 Yasui, Y. (2022). Evolutionary bet-hedging reconsidered: what is the mean–variance trade-
968 off of fitness? *Ecological Research* 37, 406–420. <https://doi.org/10.1111/1440-1703.12303>

969

970 Yoshimura, J., and Clark, C. W. (1991). *W*Individual adaptations in stochastic environments.
971 *Evolutionary Ecology* 5, 173–192. <https://doi.org/10.1007/BF02270833>

SUPPLEMENTARY INFORMATION

1
2
3
4
5
6
7
8
9
10
11
12
13

Accompanying manuscript: Toward a General Theory of Heteromorphic Reproduction

Author: P. William Hughes

S1 establishes a common accounting convention for sexual and clonal outputs

S2 reconstructs the four-environment minimum-variance locus

S3 independently optimizes long-run growth in the same four-environment model.

14 **S1. Common fitness accounting for sexual and clonal reproductive outputs**

15 *S1.1. Purpose and common currency*

16 Our portfolio model can compare biologically different reproductive outputs only after we
17 express their contributions on the same investment, temporal, and fitness scales. A seed and a
18 clonal ramet cannot be compared by counting propagules: their production costs, genetic
19 transmission, establishment probabilities, and future contributions can differ. Here we work
20 through one explicit accounting convention to show how those differences enter the model. The
21 focal system is a diploid plant that can produce sexual seeds and genetically identical clonal
22 ramets. The calculation follows the A allele of a diploid parent with genotype Aa . For a
23 heterozygous parent, an offspring can receive one copy through a maternal gamete, another copy
24 through a paternal gamete if the parent also supplies pollen, or one copy through faithful clonal
25 production. This is a deliberately bounded genetic accounting example, not a universal formula
26 for the fitness of sexual reproduction.

27

28 We first count only the maternal route. Under ordinary Mendelian segregation, the probability
29 that a sexual seed receives the parental A allele through its ovule is one-half. The q_S in Equation
30 S1 therefore counts expected maternal copies per sexual seed; it does not count the complete
31 parental contribution when the same plant also fertilizes that seed.

32

$$33 \quad q_S = \frac{1}{2} \quad (S1)$$

34

35 If a ramet faithfully copies the heterozygous parental genotype, it receives the same focal A copy
36 with probability one. This comparison assumes no somatic mutation or segregation during clonal
37 production.

38

$$39 \quad q_c = 1 \quad (S2)$$

40

41 These quantities refer to different inheritance routes for one specified parental genotype; neither
42 is a blanket discount on the demographic fitness of an offspring. If the focal heterozygote self-
43 fertilizes, the maternal gamete contributes 0.5 expected copies of A and its paternal gamete
44 contributes another 0.5, so the expected *total* parental transmission is $q_{S,\text{total}} = q_{\text{ovule}} +$
45 $q_{\text{pollen}} = 0.5 + 0.5 = 1$. This counts the expected allele copies, not the probability that a selfed
46 offspring carries A: the offspring may carry zero, one, or two copies. For an outcrossed seed with
47 pollen supplied by another parent, only the focal parent's maternal route is credited to that
48 parent's output; the other parent's genetic contribution is not credited to the focal parent. If the
49 focal parent supplies pollen elsewhere, those contributions require their own reproductive route
50 or must be included consistently within the accounting unit. A genetically identical ramet
51 carrying A contributes one copy at its initial census. We do not compare maternal-only seed
52 transmission against total parental transmission for another output and call it a biological
53 difference between mechanisms.

54

55 For an entire hermaphroditic parent's genetic return, the accounting unit includes focal allele
56 copies transmitted through ovules, through pollen fertilizing other individuals, and through
57 clonal outputs. A maternal-only comparison is legitimate when the uncredited male function is

explicitly outside the bounded accounting unit or is modeled separately. The genetic contribution of a pollen donor other than the focal parent must never be credited to the focal parent. For self-fertilization, the parent's two gametic routes contribute an expected total of one focal-allele copy before establishment and later performance are counted.

62

63 *S1.2. Production costs and allocation*

Let B denote the fixed reproductive budget available over a defined production interval. We measure the costs of the two outputs in the same limiting resource. Producing one sexual seed costs c_S ; producing one clonal ramet costs c_C . Let x_S and x_C be the proportions of B assigned to the outputs. If production is proportional to investment and the costs do not depend on allocation, the numbers produced follow by dividing each allocation by its per-offspring cost.

69

Production costs must follow the same boundary as genetic credits. When we credit both maternal and paternal transmission, the cost assigned to sexual reproduction must include the associated seed and pollen investments, including pollen sent to seeds produced elsewhere. A pollen output counted separately must not also be charged to the seed route, and pollen discounting can change the return of male function. When only maternal seed return is considered, the corresponding restricted budget must be distinguished from the complete parental reproductive budget; they cannot be interchanged in an optimization without recalibration.

77

$$78 \quad N_S = \frac{Bx_S}{c_S} \quad (S3)$$

$$79 \quad N_C = \frac{Bx_C}{c_C} \quad (S4)$$

80

81 Because we are dividing a fixed budget between the two outputs, the allocation fractions sum to
82 one:

$$83 \quad x_S + x_C = 1 \quad (S5)$$

84

85 We have now separated how much the parent invests from how many reproductive outputs that
86 investment produces. A ramet may contain more of the tracked genetic material per offspring yet
87 yield fewer offspring for the same resource expenditure.

88

89 *S1.3. Establishment, subsequent contribution, and a common time*

90 We next compare offspring that may establish at different times or survive through different
91 stages. Choose a reference census T , or an equivalent reproductive-value reference for the same
92 lineage and genetic process. Let $s_S(e)$ and $s_C(e)$ denote establishment probabilities in
93 environment e , conditional on the specified output types. Let $v_S(e, T)$ and $v_C(e, T)$ be expected
94 value per transmitted focal copy, conditional on establishment, at the shared census. The
95 products below assume that the stated establishment probabilities and per-copy census values
96 have been conditioned consistently; if different genotypes have different establishment
97 probabilities, calculate the joint expectation over genotype and survival rather than multiplying
98 separate marginal averages. Conditional values may include subsequent survival and
99 reproduction, but those same events must not be counted again elsewhere.

100

101 For a produced sexual seed, multiply the probability of focal-copy transmission, the probability
102 of establishment, and the conditional contribution at the census:

103

$$V_S(e, T) = q_S s_S(e) v_S(e, T) \quad (S6)$$

105

106 For an outcrossed seed whose maternal transmission is the only contribution credited to the focal
107 parent, insert the value from Equation S1:

108

$$V_S(e, T) = \frac{1}{2} s_S(e) v_S(e, T) \quad (S7)$$

110

111 We follow precisely the same operation for a ramet:

$$V_C(e, T) = q_C s_C(e) v_C(e, T) \quad (S8)$$

113

114 With faithful clonal inheritance, q_C equals one, giving:

$$V_C(e, T) = s_C(e) v_C(e, T) \quad (S9)$$

116

117 At an early census, v can be one per surviving focal allele copy. At a later census, the
118 contribution must incorporate the intervening genetic and demographic processes. For a selfed
119 seed, use the total expected transmission of one copy instead of the maternal-only factor of 0.5,
120 subject to the same conditioning and reference-census rules. The requirement is not identical
121 seed and ramet life histories; it is consistent accounting for the parental contribution we have
122 chosen to measure.

123

124 For selfed offspring, establishment and subsequent value must also be estimated for their actual
125 genotypes: inbreeding depression, if present, changes the return and is not captured by changing

the transmission coefficient alone. Any adult survival carried over to the census must be included once in the lineage-growth calculation rather than credited to multiple propagules.

S1.4. Returns per unit reproductive investment

The reproductive portfolio is an allocation of resources. We therefore convert each offspring contribution into a return per unit of the resource consumed. For a sexual seed, divide its expected contribution by the cost of producing it:

$$R_S(e, T) = \frac{V_S(e, T)}{c_S} \quad (\text{S10})$$

Replacing V_S by Equation S7 gives the return for the maternal-only, outcrossed-seed convention:

$$R_S(e, T) = \frac{s_S(e)v_S(e, T)}{2c_S} \quad (\text{S11})$$

The same calculation applies to clonal propagation:

$$R_C(e, T) = \frac{V_C(e, T)}{c_C} \quad (\text{S12})$$

$$R_C(e, T) = \frac{s_C(e)v_C(e, T)}{c_C} \quad (\text{S13})$$

Equations S11 and S13 express the specified contributions per unit reproductive investment at the same reference census. They do not imply that every sexual seed has the factor 0.5: if the focal parent produces a selfed seed, its expected total parental contribution enters with transmission weight one, and the sexual return becomes $R_{S,\text{self}}(e, T) = s_S(e)v_S(e, T)/c_S$ under the same conditioning assumptions. The fitness currency and the set of parental routes being credited must be specified before comparing mechanisms.

148 When paternal transmission is credited, the denominator must include the corresponding pollen
 149 cost and any resource investment needed to achieve siring success. Selfed and outcrossed seeds
 150 can also differ in establishment or later value. Thus, neither a doubling of transmission weight at
 151 unchanged cost nor a universal sexual-versus-clonal conversion factor follows from this
 152 accounting.

153

154 *S1.5. Worked accounting example*

155 We begin with a deliberately restricted maternal-route calculation. Suppose a seed costs one
 156 resource unit of maternal investment, establishes with probability 0.4, and receives the focal
 157 maternal allele copy with probability 0.5. A ramet costs two units, establishes with probability
 158 0.6, and carries one copy. The census value per established copy is one. These costs describe this
 159 bounded maternal output comparison, not the full male-plus-female reproductive budget of a
 160 hermaphrodite.

161

Component	Sexual seed	Clonal ramet
Production cost	1	2
Establishment probability	0.4	0.6
Credited expected focal copies per output	0.5 (maternal only)	1
Conditional reference-census value	1	1

162

163 The sexual return is the probability of establishment times the probability of transmission,
 164 divided by the production cost:

$$165 \quad R_S = \frac{0.4 \times 0.5}{1} = 0.20 \quad (\text{S14})$$

166

167 Using the identical resource and census accounting, the ramet produces:

$$168 \quad R_C = \frac{0.6 \times 1}{2} = 0.30 \quad (\text{S15})$$

169

170 Under the maternal-only convention, the seed yields 0.20 expected allele copies per investment
171 unit and the ramet yields 0.30. For a distinct selfing scenario, suppose pollen needed to self-
172 fertilize each seed costs an additional 0.5 resource units. Counting both the ovule and pollen
173 routes gives one expected focal copy per selfed seed; with establishment 0.4 and total sexual cost
174 1.5, its return is approximately 0.267, still below the ramet's 0.30. These figures assume
175 unchanged establishment for illustration only; inbreeding depression or other genotype-specific
176 effects would require new estimates. The apparent reversal to 0.40 that would follow from
177 adding pollen credit while leaving seed cost at one is not a valid full-budget comparison. We
178 must estimate both genetic benefits and all associated costs before ranking reproductive routes.
179

180 *S1.6. From individual returns to a reproductive portfolio*

181 To construct the portfolio, multiply the number of outputs generated by each investment by that
182 output's expected contribution. Summing the sexual and clonal components gives the total
183 expected focal-copy contribution attributable to the reproductive budget:

$$184 \quad V_P(e, T) = \frac{Bx_S}{c_S} V_S(e, T) + \frac{Bx_C}{c_C} V_C(e, T) \quad (\text{S16})$$

185

186 We next divide the complete expression by the shared budget B . This converts the result from
187 total contribution into contribution per unit investment:

$$188 \quad \frac{V_P(e, T)}{B} = x_S \frac{V_S(e, T)}{c_S} + x_C \frac{V_C(e, T)}{c_C} \quad (\text{S17})$$

189

190 Using the definitions of R_S and R_C yields the additive portfolio equation:

$$191 \quad W_P(e, T) = x_S R_S(e, T) + x_C R_C(e, T) \quad (S18)$$

192

193 The two outputs can now be combined on a common reproductive-value scale. For the
194 geometric-growth analysis in S3, an additional demographic calibration is necessary: W_P must
195 represent a positive per-generation multiplier of the same tracked lineage, not simply an
196 unnormalized count of transmitted copies per resource unit. One operational route is to measure
197 offspring contributions at a shared census relative to the lineage abundance entering the
198 reproductive interval, including any parental survival or other return components under a
199 consistent rule. If this calibration multiplies all allocations by a positive constant independent of
200 allocation and environment, the optimal allocation and relative variance comparisons are
201 unchanged. An environment-specific common factor preserves the log-optimal allocation but
202 generally changes the mean and covariance and must be retained in the corresponding risk
203 calculation. Additive parental survival can be incorporated once in the total multiplier but cannot
204 simply be discarded before calculating optimal allocation. In the four-state illustration, we
205 stipulate that the entries of R are already calibrated positive lineage multipliers per unit
206 investment. The S1 allele-count example demonstrates how to construct the genetic
207 contributions; it does not empirically establish that those counts equal the illustrative entries of
208 R .

209

210 A final calibration point is crucial for the numerical portfolio. Multiplying every output's return
211 by one shared positive constant changes the units of fitness but does not change the log-optimal

allocation; variances then scale with the square of that constant and mean-return targets scale with it. Multiplying only the sexual outputs, by contrast, changes their value relative to the clone and can change both the frontier and the optimal allocation. In the four-state example, if both seed columns are multiplied by a factor k and the clone column remains fixed, the clone's marginal inclusion ratio becomes approximately 1.2555 divided by k . The clone enters only when k is below approximately 1.256. Therefore this the outcome depends on biologically defensible, comparable calibration of all columns, not on a universal transmission discount for sexual offspring.

220

221 *S1.7. Shared environments and the covariance of reproductive returns*

The next question concerns environmental complementarity. Do conditions that reduce seed performance also reduce ramet performance, or can the clone compensate? Record the returns of both outputs in the same environmental states. Let μ_S and μ_C denote their expected returns. The covariance is the expectation of the product of their deviations from those means:

$$226 \text{Cov}(R_S, R_C) = \mathbb{E}[(R_S - \mu_S)(R_C - \mu_C)] \quad (\text{S19})$$

227

Because the entire portfolio is the sum of its weighted output returns, the variance of that sum contains two individual variance terms and a covariance term:

$$230 \text{Var}(W_P) = x_S^2 \sigma_S^2 + x_C^2 \sigma_C^2 + 2x_S x_C \sigma_{SC} \quad (\text{S20})$$

231

This is the two-output instance of the covariance model developed in the manuscript. It captures variation among the chosen shared environmental states. Additional offspring-level or

234 demographic stochasticity within states must be included in the full return distribution if it
235 matters for the empirical question.

236

237 ***S1.8. Connected ramets and nonadditive affects***

238 Some ramets remain physiologically connected to the parent. In that setting, their contribution
239 may include benefits to the genet and costs to other components of the genet. Counting only the
240 future offspring produced by the daughter ramet could miss those effects or double-count
241 transferred resources. Define the contribution of a specified clonal investment by comparing the
242 genet's reproductive value under that investment with a clearly defined counterfactual at the
243 same demographic reference:

244

$$245 \Delta V_C = V_{\text{genet,with } c} - V_{\text{genet,without } c} \quad (\text{S21})$$

246

247 The counterfactual must specify where the resources would otherwise go. If we have already
248 valued the opportunity cost in this difference, we do not deduct it a second time when calculating
249 net gains. When incremental returns remain approximately constant per unit allocated, we can
250 use an additive portfolio. If connected ramets alter the marginal returns to seed production or to
251 other ramets, returns depend on the full allocation and the model instead takes the more general
252 form:

253

$$254 W_p(e) = F(\mathbf{x}, e) \quad (\text{S22})$$

255

256 The simple additive portfolio is therefore an explicit biological approximation, not a property
257 imposed on every system of reproductive heteromorphism. Equations S11, S13, and S18 show
258 how to construct comparable sexual and clonal returns in the specified linear case. Other fitness
259 currencies can be used provided they are coherent across outputs, time, investments, and—where
260 log growth is the objective-lineage multiplication.

261 **S2. Minimum-variance allocation in the four-environment portfolio**

262 ***S2.1. Why we compare strategies at a fixed mean***

263 We now use the common return currency developed in S1 to ask whether adding a clonal output
264 improves an organism's reproductive opportunities. The question is not simply whether a mixed
265 strategy has lower variance: a consistently unproductive strategy could achieve that result.
266 Instead, we specify the same expected reproductive return for the seed-only system and the
267 expanded system, and identify the smallest variance each can achieve. This follows the
268 minimum-risk approach of Hughes (2018), now applied to outputs that may differ in
269 reproductive mechanism. We construct the environmental returns and their covariance, derive
270 the restricted two-seed allocation, add the clone, find the feasible minimum at each expected
271 return, and finally compare the resulting loci. Every value below is illustrative, not an estimate
272 from a particular species.

273

274 ***S2.2. Four shared environmental states***

275 Consider seed morph A, seed morph B, and clonal output C. Each row below represents one of
276 four environmental states, all assigned probability 0.25; each column gives the reproductive
277 return per unit investment in one output, expressed in the same currency and at the same
278 demographic reference. Using the same states for every output is necessary because we want to
279 calculate their joint performance, not compare unrelated samples.

280

$$281 \quad R = \begin{pmatrix} 9 & 1 & 2 \\ 1 & 4 & 2 \\ 2 & 1 & 5 \\ 7 & 2 & 4 \end{pmatrix}, \quad \boldsymbol{\pi} = (0.25, 0.25, 0.25, 0.25)^T \quad (S23)$$

282

283 We first calculate the mean return of each output. For A, we add its four returns and divide by
 284 four:

$$285 \mu_A = (9 + 1 + 2 + 7)/4 = 19/4 = 4.75. \quad (\text{S24})$$

286

287 For B, the same operation gives:

$$288 \mu_B = (1 + 4 + 1 + 2)/4 = 2. \quad (\text{S25})$$

289

290 For C:

$$291 \mu_C = (2 + 2 + 5 + 4)/4 = 13/4 = 3.25. \quad (\text{S26})$$

292

293 We collect those values into the mean-return vector. A has the greatest standalone arithmetic
 294 mean; the clone has an intermediate mean; B has the smallest.

$$295 \boldsymbol{\mu} = \begin{pmatrix} 19/4 \\ 2 \\ 13/4 \end{pmatrix}. \quad (\text{S27})$$

296

297 *S2.3. Deriving the covariance matrix from the same observations*

298 A mean does not show whether an output compensates for failures elsewhere in the portfolio. We
 299 calculate each deviation by subtracting the output's mean from its return in each environmental
 300 state. The resulting rows of the centered return matrix are, in the order A, B, C:

301

$$302 D = R - \mathbf{1}\boldsymbol{\mu}^\top = \begin{pmatrix} 17/4 & -1 & -5/4 \\ -15/4 & 2 & -5/4 \\ -11/4 & -1 & 7/4 \\ 9/4 & 0 & 3/4 \end{pmatrix}. \quad (\text{S28})$$

303

304 For equally probable states, each covariance is the mean product of the two corresponding
 305 columns of deviations. A variance uses a column multiplied by itself. To demonstrate the
 306 operation, the variance of A is:

$$307 \sigma_A^2 = (17^2 + (-15)^2 + (-11)^2 + 9^2)/64 = 179/16. \quad (S29)$$

308

309 The other diagonal entries follow in the same way:

$$310 \sigma_B^2 = (1 + 4 + 1 + 0)/4 = 3/2, \quad \sigma_C^2 = (25 + 25 + 49 + 9)/64 = 27/16. \quad (S30)$$

311

312 For example, the covariance of A and B is the mean of the products of their paired deviations:

$$313 \sigma_{AB} = [(17/4)(-1) + (-15/4)(2) + (-11/4)(-1) + (9/4)(0)]/4 = -9/4. \quad (S31)$$

314

315 The remaining paired calculations give:

$$316 \sigma_{AC} = [-85 + 75 - 77 + 27]/64 = -15/16, \quad \sigma_{BC} = [5 - 10 - 7 + 0]/16 = -3/4. (S32)$$

317

318 Combining the three variances and the three covariances, and placing each covariance

319 symmetrically, yields:

$$320 \Sigma = D^T D/4 = \begin{pmatrix} 179/16 & -9/4 & -15/16 \\ -9/4 & 3/2 & -3/4 \\ -15/16 & -3/4 & 27/16 \end{pmatrix}. \quad (S33)$$

321

322 The covariance matrix has full rank. Its determinant is nine and its leading principal minors are

323 positive, so there is no nonzero allocation direction along which all environmental deviations

324 vanish. The illustrative return matrix therefore contains no exactly constant-return portfolio.

325 *S2.4. The seed-only minimum-variance benchmark*

326 We first restrict the organism to A and B. If A receives fraction a , B necessarily receives $1 - a$,
 327 and C receives nothing. Their different mean returns determine which seed mixture attains a
 328 chosen portfolio mean M .

$$329 \quad \mathbf{x}_{AB} = \begin{pmatrix} a \\ 1 - a \\ 0 \end{pmatrix}, \quad M = (19/4)a + 2(1 - a). \quad (\text{S34})$$

330

331 Expand the mean constraint, collect terms in a , subtract two, and solve:

$$332 \quad M = 2 + (11/4)a, \quad a = (4M - 8)/11. \quad (\text{S35})$$

333

334 The remaining investment is then:

$$335 \quad 1 - a = (19 - 4M)/11. \quad (\text{S36})$$

336

337 Both fractions are nonnegative precisely when the target mean is between the smaller and larger
 338 standalone seed means:

$$339 \quad 2 \leq M \leq 19/4. \quad (\text{S37})$$

340

341 At any chosen mean in this interval there is only one feasible seed-only mixture. We calculate its
 342 environmental returns directly from the first two columns of R :

$$343 \quad \mathbf{w}_{AB}(a) = \begin{pmatrix} 1 + 8a \\ 4 - 3a \\ 1 + a \\ 2 + 5a \end{pmatrix}. \quad (\text{S38})$$

344

345 Substitute the expression for a in terms of M . This gives the four returns for the unique seed-
 346 only portfolio with that expected mean:

$$347 \quad W_{AB}(M) = \begin{pmatrix} (32M - 53)/11 \\ (68 - 12M)/11 \\ (4M + 3)/11 \\ (20M - 18)/11 \end{pmatrix}. \quad (S39)$$

348

349 To obtain its variance, subtract M from each environmental return, square each deviation, and
 350 average the four squared deviations:

$$351 \quad V_{AB}(M) = \frac{1}{4} \left[\left(\frac{21M-53}{11} \right)^2 + \left(\frac{68-23M}{11} \right)^2 + \left(\frac{3-7M}{11} \right)^2 + \left(\frac{9M-18}{11} \right)^2 \right]. \quad (S40)$$

352

353 Expanding the squares and gathering the terms in M gives the seed-only benchmark used in the
 354 manuscript:

$$355 \quad V_{AB}(M) = (50M^2 - 260M + 353)/22. \quad (S41)$$

356

357 ***S2.5. Adding C while preserving the same expected return***

358 We now allow C to receive a fraction t of the reproductive budget. Write a and b for the two
 359 seed allocations. The investment constraint and fixed-mean constraint provide two equations:

$$360 \quad a + b + t = 1, \quad (19/4)a + 2b + (13/4)t = M. \quad (S42)$$

361

362 Multiply the budget equation by two and subtract it from the mean equation. The B terms cancel,
 363 leaving $(11/4)a + (5/4)t = M - 2$. Multiplying by four and solving for A gives:

$$364 \quad 11a + 5t = 4M - 8, \quad a = (4M - 5t - 8)/11. \quad (S42)$$

365

366

367 Substitute this allocation into $b = 1 - a - t$ and collect terms:

368 $b = (19 - 4M - 6t)/11.$ (S44)

369

370 We have thereby expressed the entire allocation at a chosen mean using only the clone fraction

371 as a free variable:

372 $\mathbf{x}(M, t) = \begin{pmatrix} (4M - 5t - 8)/11 \\ (19 - 4M - 6t)/11 \\ t \end{pmatrix}.$ (S45)

373

374 Because the organism cannot make a negative investment, the clone fraction is bounded above

375 by whichever seed allocation would otherwise reach zero first. From $a \geq 0$, we obtain $t \leq$

376 $(4M - 8)/5$; from $b \geq 0$, we obtain $t \leq (19 - 4M)/6$. Together with $t \geq 0$, the feasible

377 interval is:

378 $0 \leq t \leq \min\{(4M - 8)/5, (19 - 4M)/6\}.$ (S46)

379

380 Setting $t = 0$ recovers the seed-only mixture, so we are comparing the original choice set with a

381 genuinely expanded one at each feasible mean.

382

383 *S2.6. Calculating expanded-portfolio variance*

384 We next substitute the three allocations into each row of the return matrix. For the first

385 environment, we multiply the allocation to A by nine, add the allocation to B, and add twice the

386 allocation to C. Collecting the terms gives the first line below; the other three lines follow by the

387 same operation:

$$\begin{aligned}
W_1 &= 9a + b + 2t = (32M - 29t - 53)/11, \\
W_2 &= a + 4b + 2t = (68 - 12M - 7t)/11, \\
W_3 &= 2a + b + 5t = (4M + 39t + 3)/11, \\
W_4 &= 7a + 2b + 4t = ((20M - 3t - 18)/11.
\end{aligned} \tag{S47}$$

389

390 The average of these four expressions equals M because we imposed the mean constraint.

391 Subtracting M from each gives the deviations used in the variance calculation:

$$\begin{aligned}
W_1 - M &= (21M - 29t - 53)/11, \\
W_2 - M &= (68 - 23M - 7t)/11, \\
W_3 - M &= (3 - 7M + 39t)/11, \\
W_4 - M &= (9M - 3t - 18)/11.
\end{aligned} \tag{S48}$$

393

394 As in the seed-only calculation, square the four deviations and average them. We write out the

395 unexpanded expression so that the source of the final polynomial is visible:

$$V(M, t) = \frac{(21M - 29t - 53)^2 + (68 - 23M - 7t)^2 + (3 - 7M + 39t)^2 + (9M - 3t - 18)^2}{484}. \tag{S49}$$

397

398 Expand, combine like terms, and simplify. The resulting quadratic is the expanded portfolio's

399 variance at fixed expected return:

$$V(M, t) = (50M^2 - 68Mt - 260M + 110t^2 + 112t + 353)/22. \tag{S50}$$

401

402 As a check, setting $t = 0$ yields the seed-only expression derived above. The comparison

403 therefore changes only access to the clonal output, not the fitness target or environmental data.

404

405 ***S2.7. Choosing clone investment that minimizes variance***

406 For any fixed target M , the only remaining choice is t . To find the unconstrained minimum,
407 differentiate the expanded variance with respect to t , keeping M fixed. Only the terms involving
408 t contribute:

409
$$\frac{\partial v}{\partial t} = (-68M + 220t + 112)/22 = 2(-17M + 55t + 28)/11. \quad (\text{S51})$$

410

411 Set this derivative to zero, transfer the other terms to the right-hand side, and solve for the clone
412 fraction:

413
$$55t = 17M - 28, \quad t_0(M) = (17M - 28)/55. \quad (\text{S52})$$

414

415 A second derivative confirms that the stationary value is the unique minimum along the constant-
416 mean line:

417
$$\frac{\partial^2 v}{\partial t^2} = 10 > 0. \quad (\text{S53})$$

418

419 The unconstrained solution must also respect the nonnegative allocations derived in S2.5. If it
420 exceeds either upper boundary, the minimum occurs at that boundary. Thus the biologically
421 feasible minimum-variance clone fraction is:

422
$$t^*(M) = \max\{0, \min[(17M - 28)/55, (4M - 8)/5, (19 - 4M)/6]\}. \quad (\text{S54})$$

423

424 We then substitute $t^*(M)$ back into the expressions for a and b ; no independent optimization of
425 the two seed fractions is necessary because the mean and budget constraints already determine
426 them.

427 **S2.8. Boundary changes and the complete minimum-variance locus**

428 The composition of the optimal portfolio changes when the unconstrained clone fraction meets
 429 an allocation boundary. First, set the expression for t_0 equal to the boundary where seed A
 430 reaches zero:

$$431 \quad (17M - 28)/55 = (4M - 8)/5 \quad \Rightarrow \quad 85M - 140 = 220M - 440 \quad \Rightarrow \quad M_L = 20/9.$$

432

433 For the upper transition, equate t_0 with the boundary where seed B reaches zero:

$$434 \quad (17M - 28)/55 = (19 - 4M)/6 \quad \Rightarrow \quad 102M - 168 = 1045 - 220M \quad \Rightarrow \quad M_U =$$

$$435 \quad 1213/322. \quad (S56)$$

436

437 Below M_L , the best allocation uses B and C, so A is zero. Between the transition means, all three
 438 outputs are used. Above M_U , B is zero and the best allocation uses A and C. To obtain the
 439 complete locus, substitute the corresponding boundary or unconstrained value of t into the
 440 variance polynomial:

$$441 \quad V_3^{\min}(M) = \begin{cases} \frac{3(10M^2 - 52M + 69)}{10}, & 2 \leq M \leq 20/9, \\ \frac{3(724M^2 - 4132M + 5949)}{1210}, & 20/9 \leq M \leq 1213/322, \\ \frac{236M^2 - 1660M + 2963}{36}, & 1213/322 \leq M \leq 19/4. \end{cases} \quad (S57)$$

442

443 The formulas agree where adjacent intervals meet, so the minimum-variance locus is continuous.
 444 The term minimum-variance locus describes the lowest available variance at each prescribed
 445 arithmetic mean. Its nondominated upper-mean portion is the efficient frontier in the strict mean-
 446 variance sense.

447

448 ***S2.9. Does adding the clone improve portfolio allocation?***

449 The seed-only allocation remains available in the expanded system by choosing $t = 0$. For every
450 attainable M , the expanded minimum therefore cannot exceed the seed-only minimum. The
451 example allows us to go further and establish when the inequality is strict. Differentiate the
452 variance with respect to clone investment at the seed-only boundary:

453
$$\left. \frac{\partial V}{\partial t} \right|_{t=0} = (56 - 34M)/11. \quad (\text{S58})$$

454

455 For every mean from two to 4.75, the derivative is negative. At either extreme mean, however,
456 the investment constraints force $t = 0$: no positive clonal allocation can preserve the minimum
457 or maximum mean. At any strictly interior mean, a sufficiently small positive clone fraction is
458 feasible and lowers variance. Therefore:

459

460
$$V_3^{\min}(M) < V_{AB}(M) \quad \text{for } 2 < M < 19/4, \quad V_3^{\min} = V_{AB} \quad \text{at the two endpoints.} \quad (\text{S59})$$

461

462 This strict improvement is a feature of the stated four-state return matrix; the general feasible-set
463 result establishes only that an optional output cannot worsen the minimum.

464

465 ***S2.10. Reproducing Figure 2 at mean three***

466 We now take one interior mean, $M = 3$, and construct both minimum-variance portfolios
467 explicitly. From the seed-only formulas, $a = 4/11$ and $b = 7/11$. Multiplying the return matrix
468 by this allocation yields the four environmental returns:

469
$$\mathbf{x}_{AB}(3) = (4/11, 7/11, 0)^T, \quad \mathbf{W}_{AB}(3) = (43/11, 32/11, 15/11, 42/11)^T. \quad (\text{S60})$$

470

471 Their arithmetic mean is three. Using the seed-only variance expression:

$$472 \quad V_{AB}(3) = (50 \cdot 9 - 260 \cdot 3 + 353)/22 = 23/22 \approx 1.04545. \quad (\text{S61})$$

473

474 With the clone available, substitute three into the unconstrained allocation formula. This value

475 lies within both feasibility bounds:

$$476 \quad t^*(3) = (17 \cdot 3 - 28)/55 = 23/55 \approx 0.41818. \quad (\text{S62})$$

477

478 Substituting this into the seed allocations gives $a = 21/121$ and $b = 247/605$. Their sum with

479 the clone fraction is one, and the mean is exactly three:

$$480 \quad x_3^*(3) = (21/121, 247/605, 23/55)^T \approx (0.17355, 0.40826, 0.41818)^T. \quad (\text{S63})$$

481

482 The returns of this mixed portfolio remain unequal across states. Furthermo multiplying R by the

483 optimized allocation gives:

484

$$485 \quad W_3^*(3) = (1698/605, 1599/605, 1722/605, 2241/605)^T. \quad (\text{S64})$$

486

487 Substitution into the variance expression gives:

$$488 \quad V_3^{\min}(3) = 207/1210 \approx 0.17107. \quad (\text{S65})$$

489

490 To express the improvement relative to the seed-only system, divide the difference in variances

491 by the seed-only variance:

$$492 \quad 100 \left[1 - \frac{207/1210}{23/22} \right] = 100 \left(\frac{46}{55} \right) \approx 83.64\%. \quad (\text{S66})$$

493 This calculation reproduces the 83.6% reduction in the manuscript at unchanged arithmetic
494 mean. It does not imply that the reproductive system is risk free: the four environmental returns
495 above remain different and the minimized variance is positive.

496

497 *S2.11. Why no exactly constant-return mixture exists here*

498 For any allocation x , portfolio variance is $x^T \Sigma x$. The covariance matrix derived in S2.3 is positive
499 definite: its first two leading principal minors and determinant are, respectively, $179/16$,
500 $375/32$, and nine, all strictly positive. Thus $x^T \Sigma x > 0$ for every nonzero allocation vector. Since
501 allocations sum to one, no feasible portfolio can have zero variance. The absence of a zero-
502 variance point is therefore established from the return data, not inferred merely from having four
503 environments instead of three.

504

505 The main biological finding in this example remains the complementarity of C with the seed
506 outputs: adding an optional reproductive route changes attainable mean-variance combinations
507 without requiring that route to be individually superior.

508 S3. Long-run growth and the reoptimized reproductive portfolio

509 S3.1. A different question on the same return distribution

510 S2 identified the lowest variance that each reproductive system can achieve at a *specified*
511 arithmetic mean. We now ask which allocation maximizes growth across generations when the
512 organism can also change its mean return. This makes the growth analysis a choice on the same
513 underlying return distribution, rather than a competing description of reproduction. We calculate
514 the independently optimized seed-only and expanded portfolios, test whether C enters the
515 existing optimum, then verify the full optimum and relate it to the variance locus.

516

517 This calculation assumes that the positive, common-currency returns described in S1 have been
518 calibrated to represent per-generation multipliers of the same tracked lineage. Let N_t be the
519 tracked lineage abundance immediately before reproduction in generation t and W_t its multiplier.
520 Following the same lineage through T generations gives:

521

$$522 \quad N_T = N_0 \prod_{t=1}^T W_t. \quad (\text{S67})$$

523

524 Taking the logarithm changes the product into a sum. Divide by the number of generations to
525 obtain the time-averaged logarithmic growth rate:

526

$$527 \quad g_T = (1/T) \sum_{t=1}^T \log W_t. \quad (\text{S68})$$

528

529 For a fixed allocation with a stationary environmental distribution and an appropriate long-run
530 averaging condition, the limiting objective is expected logarithmic growth:

$$g(x) = \mathbb{E}[\log W(\mathbf{x}, E)]. \quad (\text{S69})$$

532

533 We assign probability 0.25 to each of the same four states used in S2. If the portfolio allocations
 534 are a , b , and c , the environmental multipliers are the weighted sums of their row-specific
 535 returns:

$$W(a, b, c) = \begin{pmatrix} 9a + b + 2c \\ a + 4b + 2c \\ 2a + b + 5c \\ 7a + 2b + 4c \end{pmatrix}, \quad a + b + c = 1. \quad (\text{S70})$$

537

538 Consequently, we maximize the mean of the four log multipliers:

$$g(a, b, c) = \frac{1}{4} \sum_{e=1}^4 \log W_e(a, b, c). \quad (\text{S71})$$

540

541 Every return in the matrix is positive; hence every feasible portfolio also has positive
 542 environmental returns and the logarithms are defined.

543

544 ***S3.2. Optimizing the seed-only strategy***

545 We first restrict C to zero and set $b = 1 - a$. Substituting those fractions into the return matrix
 546 gives four multipliers:

547

$$W_{AB}(a) = (1 + 8a, 4 - 3a, 1 + a, 2 + 5a)^T. \quad (\text{S72})$$

549

550 Our seed-only growth objective is therefore:

$$g_{AB}(a) = \frac{1}{4} [\log(1 + 8a) + \log(4 - 3a) + \log(1 + a) + \log(2 + 5a)]. \quad (\text{S73})$$

552

553 To find the best seed mixture, differentiate term by term. The derivative of the logarithm of a
554 return is that return's derivative divided by the return itself:

$$555 \quad 4g_{AB}'(a) = \frac{8}{1+8a} - \frac{3}{4-3a} + \frac{1}{1+a} + \frac{5}{2+5a}. \quad (\text{S74})$$

556

557 Put these terms over the common positive denominator $(1 + 8a)(4 - 3a)(1 + a)(2 + 5a)$ and
558 combine the numerator. The stationary condition becomes:

$$559 \quad -480a^3 - 69a^2 + 350a + 86 = 0. \quad (\text{S75})$$

560

561 This cubic has one root in the biologically feasible interval $0 \leq a \leq 1$. Solving it numerically
562 gives $a \approx 0.89484779$; the other two real roots are negative and require impossible allocations.

563

564 We establish that the feasible stationary point is a global maximum by taking a second
565 derivative:

$$566 \quad g_{AB}''(a) = -\frac{1}{4} \left[\frac{64}{(1+8a)^2} + \frac{9}{(4-3a)^2} + \frac{1}{(1+a)^2} + \frac{25}{(2+5a)^2} \right] < 0. \quad (\text{S76})$$

567

568 Strict negativity throughout the feasible interval makes the growth objective strictly concave.
569 Thus the independently optimized seed-only allocation is:

570

$$571 \quad \mathbf{x}_{AB}^* \approx (0.89484779, 0.10515221, 0)^T. \quad (\text{S77})$$

572

573 Multiplication by the four-state return matrix gives the environmental growth multipliers:

$$574 \quad \mathbf{W}_{AB}^* \approx (8.158782, 1.315457, 1.894848, 6.474239)^T. \quad (\text{S78})$$

575

576 Their arithmetic mean, variance, and geometric mean are calculated using the same
577 environmental probabilities as in S2:

$$578 \mu_{AB}^* = \frac{1}{4} \sum_e W_{AB,e}^* \approx 4.46083, \quad V_{AB}^* = \frac{1}{4} \sum_e (W_{AB,e}^* - \mu_{AB}^*)^2 \approx 8.55158. \quad (S79)$$

579

580 For the geometric mean, exponentiate the average log return, equivalently taking the fourth root
581 of the product of the returns:

$$582 G_{AB}^* = \exp[g(\mathbf{x}_{AB}^*)] = (\prod_{e=1}^4 W_{AB,e}^*)^{1/4} \approx 3.38740. \quad (S80)$$

583

584 These values provide the reference for evaluating the addition of C. Both strategies must be
585 independently optimized if we want to attribute a growth improvement to access to the additional
586 reproductive route.

587

588 *S3.3. Testing whether the clone adds to the optimized seed portfolio*

589 The clone's four standalone returns are 2, 2, 5, and 4. Their arithmetic and geometric means are:

$$590 \mu_C = (2 + 2 + 5 + 4)/4 = 3.25, \quad G_C = (2 \cdot 2 \cdot 5 \cdot 4)^{1/4} \approx 2.99070. \quad (S81)$$

591

592 Both are lower than the corresponding seed-only portfolio values. But an organism does not have
593 to *replace* the entire seed portfolio with C: it can move a small fraction into C while maintaining
594 the existing seed mixture. Let t denote the transferred fraction, and write the new return as:

$$595 W(t, e) = (1 - t)W_{AB}^*(e) + tR_C(e). \quad (S82)$$

596

597 Differentiate expected log growth with respect to t and evaluate it at zero, where the clone is just
 598 entering. The chain rule gives:

$$599 \left. \frac{dg}{dt} \right|_0 = \mathbb{E} \left[\frac{R_C - W_{AB}^*}{W_{AB}^*} \right] = \mathbb{E} \left[\frac{R_C}{W_{AB}^*} \right] - 1. \quad (\text{S83})$$

600

601 The clone therefore improves the existing optimum at the margin if its expected relative return
 602 exceeds one. Substituting the four environmental outcomes gives:

$$603 Q_{C|AB} = \frac{1}{4} \left[\frac{2}{8.158782} + \frac{2}{1.315457} + \frac{5}{1.894848} + \frac{4}{6.474239} \right] \approx 1.25552. \quad (\text{S84})$$

604

605 Because the value exceeds one, initial clone investment increases expected log growth. The
 606 result depends on C's return relative to the existing portfolio in each environment, rather than its
 607 standalone mean. We must still reoptimize the full allocation, because the presence of C can
 608 change how much investment remains in A and B.

609

610 *S3.4. Solving the expanded problem*

611 We maximize the same four-environment objective over nonnegative allocations that sum to one.

612 The optimum occurs on the boundary where B receives zero, but we must establish this rather
 613 than assume it. First optimize along the A–C boundary, setting $b = 0$ and $c = 1 - a$.

614 Substitution into the four environmental returns gives:

615

$$616 W_{AC}(a) = (2 + 7a, 2 - a, 5 - 3a, 4 + 3a)^\top. \quad (\text{S85})$$

617

618

619

620 We therefore maximize:

$$621 \quad g_{AC}(a) = \frac{1}{4} [\log(2 + 7a) + \log(2 - a) + \log(5 - 3a) + \log(4 + 3a)]. \quad (\text{S86})$$

622

623 We then differentiate the four logarithms:

$$624 \quad 4g_{AC}'(a) = \frac{7}{2+7a} - \frac{1}{2-a} - \frac{3}{5-3a} + \frac{3}{4+3a}. \quad (\text{S87})$$

625

626 Combine these terms over their shared denominator. The resulting polynomial equation for a

627 stationary point is:

$$628 \quad 252a^3 - 387a^2 - 280a + 252 = 0. \quad (\text{S88})$$

629

630 Its only root between zero and one is $a \approx 0.59812010$. One other real root is negative and the

631 third exceeds one. The second derivative verifies that this root is the unique maximum along the

632 A–C boundary:

$$633 \quad g_{AC}''(a) = -\frac{1}{4} \left[\frac{49}{(2+7a)^2} + \frac{1}{(2-a)^2} + \frac{9}{(5-3a)^2} + \frac{9}{(4+3a)^2} \right] < 0. \quad (\text{S89})$$

634

635 The optimized allocation on this boundary is consequently:

$$636 \quad \mathbf{x}_{AC}^* \approx (0.59812010, 0, 0.40187990)^T. \quad (\text{S90})$$

637

638 We next ask whether B could improve this boundary optimum. Define the expected relative

639 contribution of any output i to an existing portfolio W as:

$$640 \quad Q_i = \mathbb{E} \left[\frac{R_i}{W} \right]. \quad (\text{S91})$$

641

642 If an output receives positive investment at an optimum, its relative contribution is one; an
 643 excluded output must have a relative contribution no greater than one. To see why the common
 644 value equals one, weight the marginal contributions by the allocations and sum:

$$645 \sum_i x_i Q_i = \mathbb{E} \left[\frac{\sum_i x_i R_i}{W} \right] = \mathbb{E}[W/W] = 1. \quad (\text{S92})$$

646

647 Because all positive allocations have equal marginal contributions at an optimum and those
 648 allocations sum to one, each included output has $Q_i = 1$. The corresponding condition for an
 649 excluded output is $Q_i \leq 1$; otherwise replacing a small amount of an included output would
 650 improve log growth.

651

652 At the A–C optimum, B’s returns are 1, 4, 1, and 2. We evaluate its marginal contribution in the
 653 existing environmental portfolio:

$$654 Q_B = \frac{1}{4} \left[\frac{1}{W_{AC,1}^*} + \frac{4}{W_{AC,2}^*} + \frac{1}{W_{AC,3}^*} + \frac{2}{W_{AC,4}^*} \right] \approx 0.91801 < 1. \quad (\text{S93})$$

655

656 The included outputs A and C satisfy $Q_A = Q_C = 1$ to numerical precision. Since the logarithm
 657 of a positive affine return is concave and averages of concave functions are concave, these
 658 conditions establish global optimality across the entire three-output simplex. Thus the full
 659 optimum is exactly the A–C boundary solution found above; it is not just the best portfolio
 660 within an arbitrarily chosen two-output subset.

661

662 ***S3.5. Growth and variance at the expanded optimum***

663 Substituting the full allocation into the environmental returns gives:

$$664 W_{ABC}^* \approx (6.186839, 1.401880, 3.205640, 5.794360)^T. \quad (\text{S94})$$

665

666 Calculate its arithmetic mean and environmental variance with the same probabilities used
667 throughout:

$$668 \mu_{ABC}^* = \frac{1}{4} \sum_e W_{ABC,e}^* \approx 4.14718, \quad V_{ABC}^* = \frac{1}{4} \sum_e (W_{ABC,e}^* - \mu_{ABC}^*)^2 \approx 3.82414. \quad (\text{S95})$$

669

670 Its geometric mean return is:

$$671 G_{ABC}^* = \left(\prod_{e=1}^4 W_{ABC,e}^* \right)^{1/4} \approx 3.56266. \quad (\text{S96})$$

672

673 We now compare the independently optimized full strategy against the independently optimized
674 seed-only strategy. The proportional change in geometric mean is:

$$675 100(G_{ABC}^*/G_{AB}^* - 1) \approx 5.17\%. \quad (\text{S97})$$

676

677 The arithmetic mean falls by approximately 7.03%, while variance falls by approximately
678 55.28%. Geometric mean growth nevertheless increases. This is a concrete illustration of the
679 connection between variable reproductive performance and long-run success; it does not, by
680 itself, establish that any observed natural reproductive mixture evolved through bet hedging.

681

682 ***S3.6. Connecting the growth optimum to the fixed-mean frontier***

683 S2 compared risk-minimizing portfolios at mean three, whereas S3 has selected an allocation
684 with arithmetic mean approximately 4.147. It would be misleading to compare those allocations
685 as though they competed at one prescribed mean. We instead evaluate the minimum-variance
686 solution at the log optimum's own mean. Inserting $M \approx 4.14718$ into the feasible clone upper
687 bound gives:

$$t_{\max}(M) = (19 - 4M)/6 \approx 0.40188. \quad (\text{S98})$$

689

690 The unconstrained variance minimum at that mean would use a larger clone fraction and would
 691 require a negative allocation to B; hence the feasible minimum sits at $b = 0$, with the same A–C
 692 allocations found by the log-growth optimization. Equivalently, substitution of the log
 693 optimum’s mean into the upper branch of the piecewise minimum-variance locus gives its
 694 variance ≈ 3.82414 .

695

696 The log-optimal point therefore lies on the minimum-variance locus at its own arithmetic mean
 697 in this example. This agreement is a calculated property of the illustrated return distribution, not
 698 a universal equivalence of minimizing variance and maximizing expected log growth. The two
 699 analyses supply complementary information: the locus displays the attainable trade-off at each
 700 mean, and expected log growth selects the evolutionary optimum under the specified
 701 multiplicative model.

702

703 *S3.7. The allocation consequence for an existing seed morph*

704 The seed-only optimum invests approximately 10.5% in B. After C becomes available, the
 705 reoptimized strategy invests nothing in B. B’s four environmental returns have not changed; its
 706 marginal contribution has changed because the competing strategy now contains C. The value
 707 $Q_B \approx 0.918$ provides a non-marginal exclusion result in this illustrative matrix, while the general
 708 threshold is given by the inequality $Q_B \leq 1$.

709

710 This finding concerns optimal investment, not the developmental loss of a seed morph or a
711 prediction that all new reproductive mechanisms displace existing ones. It illustrates the broader
712 conclusion that each output's value is contingent on the complete set of available reproductive
713 alternatives.

714

715 ***S3.8. Reproducibility and scope***

716 Every number reported in S2 and S3 is determined by the stated four-by-three return matrix, the
717 four equal environmental probabilities, the budget constraint, and either the fixed-mean variance
718 or expected-log-growth objective. All covariance entries use population probabilities (division
719 by four), not a sample covariance correction. The seed-only and full growth optima were
720 obtained by solving the one-dimensional stationary polynomials and checking the excluded-
721 output condition; the piecewise risk minima were obtained by differentiating a convex quadratic
722 and applying the allocation bounds.

723

724 These calculations concern environmental variation in positive lineage multipliers. Offspring-
725 level demographic stochasticity, inherited variation in allocation, age structure, and allocation-
726 dependent physiological returns are not estimated in this numerical example. Nonlinear returns
727 can be represented by a more general allocation-dependent function, but their optimality
728 conditions need not equal the linear expressions above.

729

730 Taken together, the supplementary derivations show how a common fitness currency supports
731 the reproductive return matrix, how the matrix determines the minimum-variance locus, and how

732 the same environmental returns identify the independently optimized long-run reproductive
733 strategy.

734

735

736

737