Seasonality and competition select for variable germination behavior in perennials

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Abstract: The common occurrence of within-population variation in germination behavior and associated traits such as seed size has long fascinated evolutionary ecologists. In annuals, unpredictable environments are known to select for bet-hedging strategies causing variation in dormancy duration and germination strategies. Variation in germination timing and associated traits is also commonly observed in perennials, and often tracks gradients of environmental predictability. Although bet-hedging is thought to occur less frequently in long-lived organisms, these observations suggest a role of bet-hedging strategies in perennials occupying unpredictable environments. We use complementary numerical and evolutionary simulation models of within- and among-individual variation in germination behavior in seasonal environments to show how bet-hedging interacts with density dependence, life-history traits, and priority effects due to competitive differences among germination strategies. We reveal substantial scope for bet-hedging to produce variation in germination behavior in long-lived plants, when "false starts" to the growing season results in either competitive advantages or increased mortality risk for alternative germination strategies. Additionally, we find that two distinct germination strategies can evolve and coexist through negative frequency-dependent selection. These models extend insights from bet-hedging theory to perennials and explore how competitive communities may be affected by ongoing changes in climate and seasonality patterns.

Introduction

Accurate timing of seasonal phenology is key to population persistence in unpredictable environments. The timing of emergence can have strong and direct effects on individual fitness, and is expected to be subject to strong selection driving local adaptation (Donohue et al. 2010). Indeed, emergence behavior (e.g. patterns of germination or hatching) is often found to vary in predictable ways along environmental gradients (Meyer et al. 1995; Venable 2007; Wagmann et al. 2012; Simons 2014; Pinceel et al. 2017; Rubio de Casas et al. 2017;

Torres-Martínez et al. 2017; Scholl et al. 2020). In most plants and many animals, the timing of emergence is controlled by dormancy (Vleeshouwers et al. 1995; Finch-Savage and Leubner-Metzger 2006; Baskin and Baskin 2014), and the evolution of emergence behavior is thus tightly linked to the evolution of dormancy mechanisms (Varpe 2017).

Theoretical models of seed dormancy and germination behavior have a long history (Cohen 1966; Venable and Lawlor 1980; Ellner 1985; Geritz et al. 2018; Hughes 2018; Kortessis and Chesson 2019). Most of these, however, have focused on specific systems such as annual plants in desert environments. This system provides a natural starting point because one striking observation demands an explanation: a fraction of the seeds produced each year fail to germinate the next year, and instead lie dormant for another year before germinating at the beginning of the second growing season following their dispersal (Gremer and Venable 2014). While this reduction in number of seedlings may seem a waste of resources most years, such a strategy has been identified as a risk-spreading adaptation to avoid complete recruitment failure in the event of a bad year. Prolonged seed dormancy and variation in germination timing have come to represent the archetype of a bet-hedging strategy, i.e. a genotype-level strategy that sacrifices some short-term (arithmetic-mean) fitness gains in order to lower its fitness variance over time (Levins 1962; Cohen 1966; Venable 2007). Such bet-hedging strategies have received considerable empirical and theoretical attention as a major mode of adaptation to unpredictable environments (Seger and Brockmann 1987; Simons 2011; Starrfelt and Kokko 2012).

Empirical and theoretical studies of bet-hedging have yielded a good understanding of how different types of risk-spreading adaptations co-evolve, interact, and cancel each other out. For example, if phenotypic polymorphisms or continuous variation ensures that fitness correlations among related individuals are sufficiently low, then there is less need for other costly bet-hedging strategies at the individual level such as 'safer' offspring phenotypes that are weaker competitors but better able to cope with environmental variation (Venable and Brown 1988; Starrfelt and Kokko 2012; Haaland et al. 2020; Escobar et al. 2021). The scope for bet-hedging is also lowered if the spatiotemporal scale of environmental variation (what is often called environmental 'grain' in bet-hedging terms) already ensures that individuals in a population experience different conditions and thus uncorrelated fitness returns. In a spatially fine-grained environment the population is exposed to a wide range of different conditions at any given time (as opposed to coarse-grained environments where all individuals experience the same conditions), and in such cases, genotype-level diversification or other bet-hedging strategies are not selectively favored (Levins 1962; Starrfelt and Kokko 2012). Furthermore, longer lifespans with a larger number of selective events over which fitness can accumulate (e.g. an individual experiencing multiple consecutive breeding seasons with variable conditions) also reduces the need for any variance reduction if fitness payoffs among selective events are uncorrelated (Haaland et al. 2019).

Given these insights, it is unsurprising that most models of bet-hedging, as well as many of the best-documented empirical examples, consider rather specific types of short-lived organisms with discrete generations occupying highly variable, coarse-grained environments, such as germination strategies of desert annuals, or overwintering strategies for organisms living in ephemeral ponds (Furness et al. 2015; García-Roger et al. 2016; Wang and Rogers 2018). However, this focus has also led to a knowledge gap regarding the evolution of seemingly 'risk-spreading' traits in longer-lived organisms, as these may require other

explanations than bet-hedging in its strictest sense. Variation in seed germination behavior is seen not only in annuals, and is at least sometimes associated with variation in seed size (Rees 1996; Simons and Johnston 2000; Susko and Lovett-Doust 2000; Norden et al. 2009; Harel et al. 2011; Martins et al. 2019). A classic example of within-individual variation in seed size is seed heteromorphism, as observed e.g. in many Asteraceae and Chenopodiaceae (reviewed in Venable 1985; Imbert 2002), where distinct seed morphs differ in their dispersal abilities and germination behavior (Venable et al. 1987; Brändel 2004; Fumanal et al. 2007; Yao et al. 2010; Wang et al. 2012). Continuous variation in seed size is also common in natural populations, and may relate to variation in germination behavior (Pélabon et al. 2021). Within species, larger seeds are generally more likely to germinate and/or germinate earlier than do smaller ones (Biere 1991; Simons and Johnston 2000; Tremayne and Richards 2000; Galloway 2001; Pélabon et al. 2005), but the opposite pattern of seed mass increasing the time necessary to break dormancy and induce germination is also observed (Martins et al. 2019).

Seed size variation is thus a common mechanism for producing seeds with variable duration of dormancy and/or variable germination time both within individuals as well as within an inflorescence (Pélabon et al. 2021). As argued, existing bet-hedging models alone are not able to explain the ubiquity of seed heteromorphism or continuous seed size variation as observed in perennials (Martins et al. 2019). Although several other non-mutually exclusive hypotheses exist, including but not limited to variance-sensitivity due to asymmetrical fitness costs versus benefits (Bednekoff 1996; Bårdsen et al. 2008), fluctuating selection or fluctuations in priority effects (Chesson 2000; ten Brink et al. 2020), competitive asymmetries among offspring types (Geritz 1995) and negative frequency-dependent selection (Metcalf et al. 2015; Poethke et al. 2016), these have seldom been analyzed jointly (but see Rees et al. 2004). In Scholl et al.'s (2020) recent analysis of the flora of the south-east United States, annuals were not detectably more likely to exhibit seed heteromorphism than were perennials, suggesting that selection for within-individual variation in germination behavior may be common also in long-lived plants where bet-hedging is less strongly favored.

Here, we explore the evolution of individual variation in dormancy of long-lived plants in seasonally varying environments, using both numerical and simulation models covering a range of ecological scenarios. Our numerical model derives general predictions for when bet-hedging can favor within-plant variation in germination behavior as an adaptation to seasonal environmental variation in perennials. To this end we compare long-term arithmetic and geometric growth rates of populations exhibiting different germination strategies. This model uses a simple setup assuming two discrete seed morphs, a "small" seed with a short dormancy period, and a "large" seed with a long dormancy period. This analysis identifies the strength of priority effects and factors affecting the riskiness of early germination (probability of a "false start" and small-seed juvenile survival) as key determinants of optimal seed strategies and reveals ample scope for bet-hedging in within-plant seed variation. We complement this numerical model with individual-based evolutionary simulations of both mean and standard deviation of dormancy duration modelled as continuous traits. This model accounts for density- and frequency dependence and allows us tease apart the relative effects of bet-hedging, competition, and fluctuating selection by adjusting parameters such as lifespan, the grain of the environment, and the strength of priority effects. We let rainfall patterns vary predictably and unpredictably within and among years, emulating the wet- and dry-season dynamics seen in large parts of the tropics where intermittent dry-season rains can trigger germination of certain seed types. However, we note that this model setup applies equally

well to other stochastic seasonal changes between harsh and favorable conditions, such as the onset of warmer spring weather in temperate regions where "false starts" of warm temperatures may still be followed by harmful frosts.

1. Selection for within-plant variation in germination behavior

Model setup

We first present a numerical model where we assume that plants can produce two seed morphs, here "small" and "large" seeds, that differ in the amount of rainfall required for germinating. Each year consists of a dry and a wet season, and with probability p_f there is some intermittent rainfall (a "false start") during the dry season, which triggers germination of small seeds. These early seedlings emerging during intermittent rains have a high probability of dying due to drought, and therefore only a small chance to recruit into the adult population during such years. Large seeds, on the other hand, require more rainfall in order to germinate, and therefore remain dormant through any intermittent rains. When the wet season begins, small seeds have a competitive advantage over large seeds (given that there was no intermittent rain during the dry season) because they germinate faster, giving the seedlings a head start to growth, and thus a higher probability of recruitment into the adult population.

We designate as f the fraction of small seeds produced by a plant, so that a fraction 1-f are large seeds. Assuming no density- or frequency-dependence, the equations for population growth in the two different types of years (with or without false rains) become

$$N(t+1)_{\text{false}} = N(t)s_{\text{a}} + N(t)y[(1-f) + fs_{\text{juv}}]$$

(eq. 1)

$$N(t+1)_{\text{normal}} = N(t)s_{\text{a}} + N(t)y[(1-f)c + f]$$

where N is the number of adult plants, s_a is annual adult survival, y is seed yield per plant, f is the fraction of small seeds produced, s_{juv} is the juvenile survival of small seeds in the case of intermittent rain, and c is the relative competitive disadvantage of large seeds compared to small seeds in normal years. If c is low, small seeds benefit from a strong priority effect in terms of competition for recruitment, whereas if c is large (near 1), small and large (respectively early- and late-germinating) seeds are competitively similar in years without intermittent rain (weak priority effects).

To find the optimal strategy f^* we calculate long-term geometric growth rate λ_{geom} for a given probability p_f of years having a false start during the dry season (eq. 2). In order to identify any bet-hedging effect, we compare this strategy with the one that optimizes arithmetic mean fitness (eq. 3).

$$\lambda_{\text{geom}} = p_{\text{f}} * \log\{N(t+1)_{\text{false}}\} + (1-p_{\text{f}}) * \log\{N(t+1)_{\text{normal}}\} \qquad \text{(eq. 2)}$$

$$\lambda_{\text{arit}} = \log\{\, p_{\text{f}} * N(t+1)_{\text{false}} + (1-p_{\text{f}}) * N(t+1)_{\text{normal}}\} \qquad \text{(eq. 3)}$$

Maximizing (2) over f identifies the optimal strategy f^* leading to the highest population growth rate as a function of environmental conditions (years with or without false starts). This is calculated numerically because we do not obtain a closed-form expression for f^*.

Results

This simple model reveals that there is considerable scope for bet-hedging (optimal strategies differ depending on whether arithmetic or geometric mean growth rate is being maximized), and that there are large ranges of parameter values for which the optimal strategy is a mix of small and large seeds (Fig. 1). Arithmetic mean fitness maximization always favors a pure strategy (f^* = 0 or 1), and the transition between parameter spaces favoring one or the other is indicated by a red line. In contrast, geometric mean fitness can favor mixed strategies,

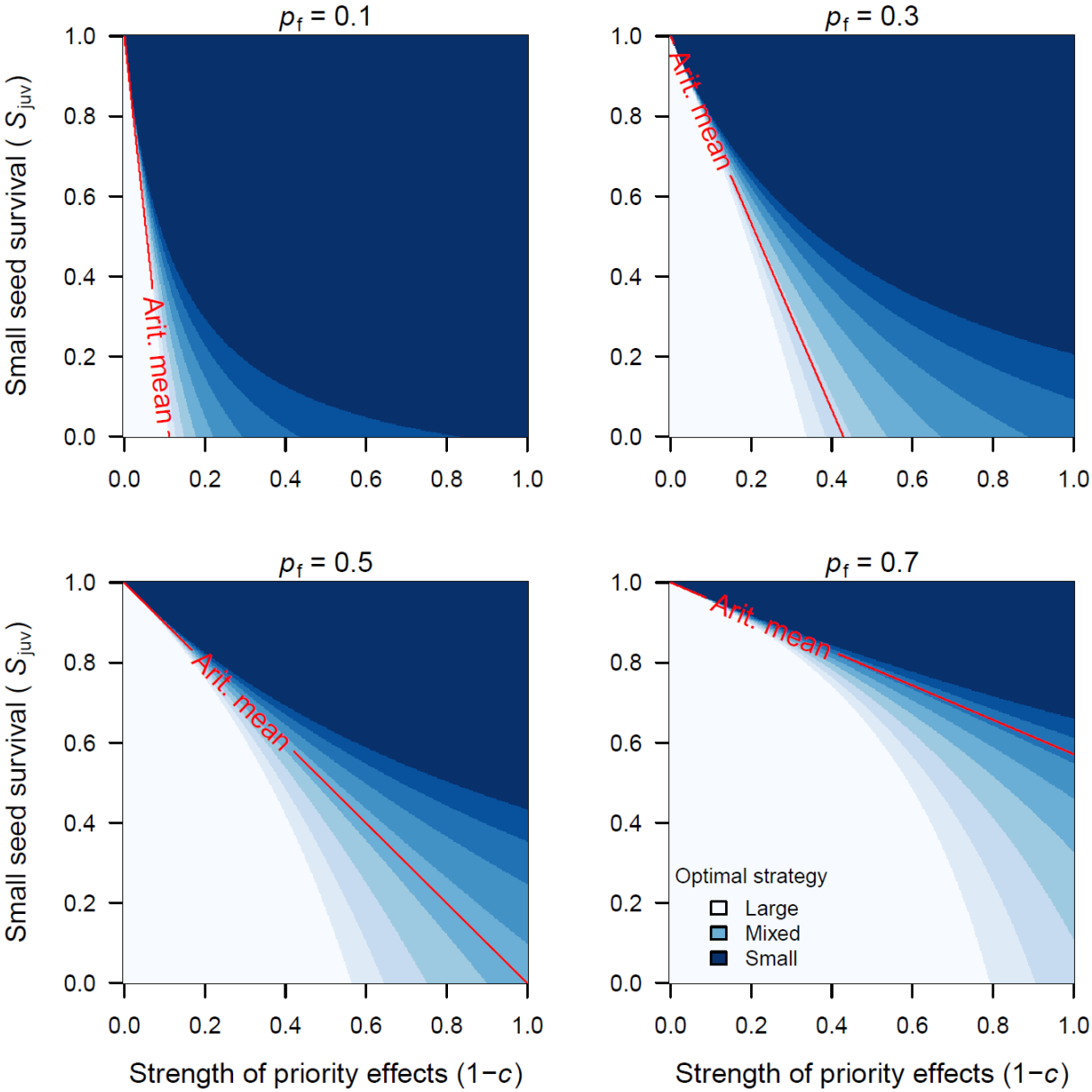

Fig. 1: Optimal fraction of small seeds (f^*) for different values of small-seed survival under false rains, s_{juv} (y-axis), strength of priority effects, 1-c (x-axis), and probabilities of false rains, p_f. The red line shows where arithmetic mean fitness maximization switches from producing only large seeds (f=0, below the line) to only small seeds (f=1, above the line). Adult survival s_a=0.9, which translates to an average adult lifespan of 10 years.

especially when the fitness difference between large and small seeds varies extensively across years. This occurs when s_{juv} is small (low juvenile survival through the dry season following intermittent rain), c is small (small seeds have a strong competitive advantage over large seeds), and p_f is intermediate (years with and without a false start are about equally likely).

2. Individual-based model of mean and variance in dormancy

Model setup

Here, we build an individual-based simulation model of the joint evolution of mean and variance in dormancy duration in perennial plants. We assume that seed germination is determined by the dormancy period d_z, which functions as an obligate "biological clock" preventing germination until a certain time d_z has passed (see table 1 for an overview of all mathematical notation and baseline parameter values used in the individual-based model). Germination of a seed occurs with probability 1 as soon as its age (in weeks) is greater than d_z and a rainfall occurs that exceeds some threshold amount R_{thres}. We here allow continuous, normally distributed within-individual variation in d_z (rather than just e.g. "small" and "large" seeds), determined by two haploid genes d_μ and d_σ that control respectively the mean and standard deviation (in weeks) of the distribution of d_z among an individual's offspring. The actual phenotypic trait value of an offspring i is thus randomly drawn from a Gaussian distribution determined by its parent's genetic values: $d_{z,\,i} \sim N(d_\mu, d_\sigma^2)$. Because week number is an integer, we handle non-integer values by probabilistically assigning germination week (i.e., given that a rainfall $R > R_{thres}$ has occurred, a seed with $d_{z,i} = 23.6$ has a 40 % chance of germinating in week 23, and 60 % chance of germinating in week 24).

Population initialization. Each replicate simulation starts with N_0 adult individuals. Each of these individuals are independently assigned a random combination of gene values, where starting d_μ values are normally distributed with a mean of 15 and standard deviation of 3 weeks, and the d_σ values with a mean of 3 and a standard deviation of 3 weeks. Negative d_σ values are set to 0. We start the simulations with ample standing genetic variation for computational purposes (but see Supplementary Material Part 2 for control simulations initialized without genetic variation).

Abiotic conditions. We model time steps of one week and assign the first 26 weeks of a year as the dry season and the last 26 weeks as the wet season. Dry-season rainfall varies stochastically within years, with 26 weekly rainfalls randomly drawn at the start of the year from a zero-mean normal distribution with variance σ^2_{within}, truncated between 0 (lowest) and 1 (highest). The actual mean and variance of these weekly rainfalls thus differ from 0 and σ^2_{within}, but larger σ^2_{within} will lead both to more weeks exceeding a given rainfall threshold R_{thres} required for seed germination and to an increase in the survival probabilities of germinated seeds (Fig. 2). Weekly rainfall in the wet season is always equal to 1.

We examine evolutionary outcomes under coarse-grained and fine-grained environmental variation. Under coarse-grained environmental variation, we assume that all seeds experience the same sequence of weekly rainfalls $\boldsymbol{R}$ (a vector of 52 values) but $\boldsymbol{R}$ differs among years. Under fine-grained environmental variation, different $\boldsymbol{R}$ vectors are assigned to individual seeds at random. Specifically, we produce 20000 sequences of weekly rainfall and assign each

seed a random $\boldsymbol{R}$ chosen among these. Thus, experienced rainfall will vary a lot among individuals within a year in this scenario, but average rainfall will vary less across years.

Survival of seedlings and adults. After setting the weekly rainfall of a particular year, we determine the survival probability of seedlings and adults in that year. We assume that survival increases both with rainfall and with the age of the plant. The probability of survival for an individual i with age $a_{i,t}$ in a given week t with rainfall R_t (or $R_{i,t}$ in the fine-grained scenario) equals

$$S_{i,t}(a_{i,t}, R_t) = \frac{S_{\min} R_t}{\mu_{\text{wet}}} + \frac{(S_{\max} - S_{\min} R_t)}{1 + \exp(-\delta_1(a_{i,t} - a_{\text{infl}}(1 - R_t \delta_2)))}, \qquad \text{(eq. 4)}$$

i.e. a sigmoid function of seedling age, the lower asymptote of which increases with increasing rainfall (Fig. 2A, B). Note that rainfall also affects the horizontal position of the function (how far "along" the x-axis the seed has come in terms of survival), and that the strength of this effect increases with the parameter δ_2.

With the rainfall data of a particular year and the survival function (eq. 4), we can now calculate each seedling's survival probability (Fig. 2C), which is given by the product of its (age- and rain-dependent) survival probabilities of each week from germination time t_{germ} until the end of the year:

$$S_i(t_{\text{germ}}, \boldsymbol{R}) = \prod_{t=t_{\text{germ}}}^{52} S_{i,t}(a_{i,t}, R_t)$$

To determine whether a seedling survives its first year, we draw a random number from a uniform distribution [0,1]. If this random number is lower than the survival probability of the seedling, the seedling will survive. Otherwise it is removed from the population. Likewise, we can calculate which of the adults will be allowed to reproduce (see below) and survive to the

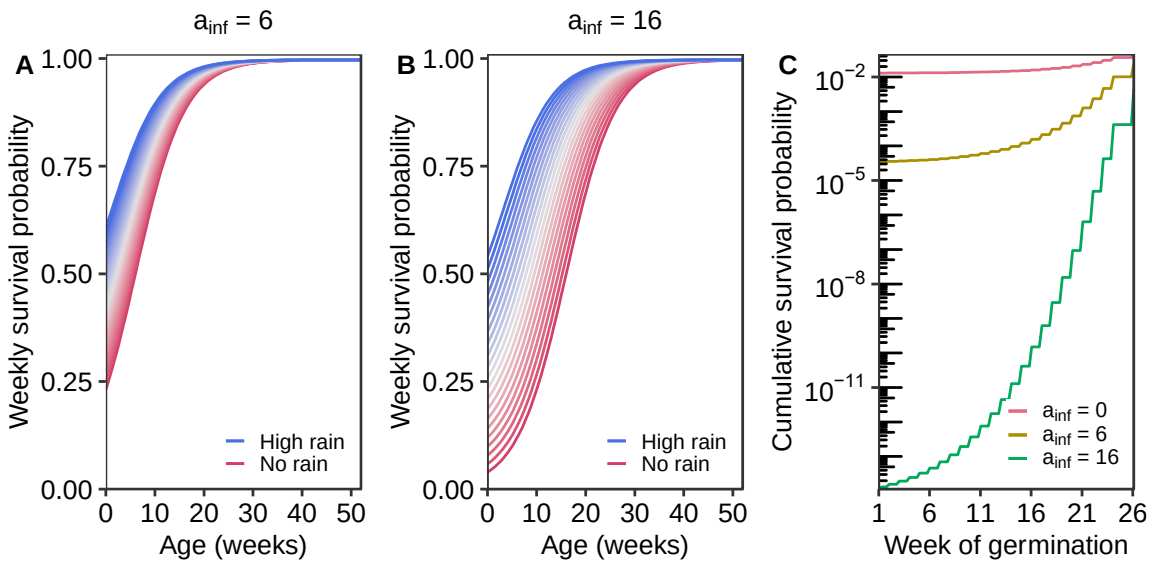

Fig. 2: Seedling survival functions. A and B: Weekly survival probability for different amounts of rainfall (blue lines: $\boldsymbol{R}$=1; red lines: $\boldsymbol{R}$=0) and varying the inflection point a_{inf} of the juvenile survival function Si,t (panels). C: Effect of week of germination (x-axis) and a_{inf} (colored lines) on the probability of a seedling surviving its first year (52 weeks since germination), assuming a worst-case scenario with no rainfall in the dry season and constant high rainfall ($\boldsymbol{R}$=1) in the wet season.

next year. We assume that survival for plants of age $a_i \geq 52$ weeks, S_{adult}, is independent of age and rainfall.

Recruitment and density dependence. We assume that only K adult plants can live in the environment. At the end of the wet season, we determine which of the seedlings that germinated in this year will recruit into the adult population. We first calculate the number of available slots (K minus the number of surviving adults), and then fill the empty slots with seedlings. Recruitment success can be either age-dependent, with slots filled sequentially by older seedlings first ('priority effects'), or age-independent, with slots filled at random.

Table 1: Overview of variables and parameters of the individual-based model.

Parameter in text	Description	Default values and range
	A) Abiotic environment parameters	
σ^2_{within}	Variance in mean weekly rainfall within a year.	We explore [0, 4].
R_t	Realized rainfall in a particular week.	[0, 1].
	B) Survival function parameters	
a	Age of seedling.	
s_{min}	Lower asymptote of the seedling survival function (survival probability given a=1 and R_t=0).	Default 0.3.
s_{max}	Upper asymptote of the seedling survival function (survival probability when a and R_t are large).	Default 0.997.
δ_1	Affects the steepness of the survival function.	Default 0.2.
δ_2	Enhances the effect of rain on the survival function.	Default 0.8.
a_{infl}	Age (weeks) at which the survival function increases most steeply.	Default 6. We also examine a_{infl} = {0, 16}.
	C) Genes and trait values	
d_μ	Genetic value determining expected (mean) seed dormancy.	-
d_σ	Genetic value determining standard deviation of seed dormancy.	-
$d_{,z,i}$	Actual individual dormancy period of seed i (in weeks).	
	D) Demographic and evolutionary parameters	
K	Carrying capacity.	Default 5000.
γ	Yearly fecundity per adult plant.	Default 50.
m	Per-locus mutation rate.	Default 0.01.
m_{size}	Size of mutational effects (The standard deviation of the Gaussian distribution from which the new trait value is chosen).	Default 0.01.
N_0	Starting population size.	Default equal to K.
c	Strength of priority effects (competitive advantage to germinating earlier). Proportion of recruitment that does not depend on seedling age.	Default 1. We also examine c = 0.
s_{adult}	Weekly adult survival probability. Yearly survival probability becomes s_{adult}^{52}. Expected lifespan (in weeks) becomes $1/(1-s_{adult})$	Default 0.997. We also examine 0.994.

Reproduction, inheritance and mutation. At the end of the wet season, all adult plants (i.e. individuals older than 52 weeks, not the juveniles that were just recruited) reproduce asexually. Individual seed production is Poisson distributed with a mean fecundity of γ. Offspring inherit their parent's gene values for determining dormancy duration (d_μ, d_σ), but not their actual phenotype d_z. Each locus has an independent probability m of experiencing mutation. Mutational effects on d_μ are of constant effect, such that the new gene value is drawn from a normal distribution with a mean equal to the previous value, and a standard deviation of m_{size}. For d_σ, whose value is bounded by 0, mutations that would lead to negative values are mirrored around 0, ensuring that the new gene value is positive.

Data generation and analysis. Simulations run for 100.000 years. We present results derived from averages over the last 1000 years (but see Fig. S2), in order to eliminate any irregularities produced by yearly environmental variation. Each scenario is replicated over 10 independent runs for course-grained environmental variation. In case of fine-grained environmental variation we replicate each scenario 3 times only because variation among replicates is negligible.

We find, under some conditions, that two strategies can coexist in the population until the end of the simulations. To aid data interpretation, we plot the trait values d_μ and d_σ and the corresponding dormancy periods d_z for each simulation and determine visually whether there are one or two clusters in trait space. If there are two clusters we use the k-means method (Hartigan & Wong, 1979) to allocate individuals to a certain cluster. This method partitions the strategies into groups so that the sum of squares from points to the assigned cluster centers is minimized. The algorithm uses random data points as starting locations to sort individuals to their nearest cluster center, so we let it run 20 times per replicate in order to minimize this randomness introduced when determining starting cluster centers. We implemented the model in C++; the code will be made available online. Simulations were run using GNU parallel (Tange 2021).

Results

Despite the added ecological and evolutionary complexity of the individual-based simulation model, we overall find that these results correspond well with those of the simpler phenomenological model (section 1). Specifically, we will present four findings that clearly demonstrate the relative effects of competition, life-history, and environmental variation in determining within- and among-individual variation in germination behaviour and associated traits. (i) In the absence of any priority effects, germination always occurs at the beginning of the wet season, because the risks of early germination are never worth taking. (ii) Adding priority effects via age-dependent competition for recruitment favors greater risk-taking, in the form of earlier germination and/or spreading of germination. We often find coexistence of multiple strategies because some years (with more favorable dry-season rainfall patterns) favor more competitive (and risky) strategies than others, i.e. potential for both within- and among-plant seed size variation. (iii) Only intermediate seedling mortality selects for mixed strategies. Any within- or among-individual dormancy variation disappears if dry-season conditions are either very benign or very harsh. (iv) Under density-dependence, long adult lifespan increases competition because fewer 'slots' are available for seedlings to colonize and eventually recruit into the adult population, leading to increased risks taken via early

germination and/or spreading of germination. Finally, alongside findings (i-iv), we investigate bet-hedging effects of genotype-level fitness variance caused by among-individual fitness correlations by comparing results obtained in temporally coarse-grained environments (all individuals experience the same rainfall patterns in a given year, resulting in high among-year variation) with those obtained in fine-grained environments (rainfall patterns are assigned independently for all individuals in a given year, resulting in low among-year variation). In fine-grained environments, we never detect any spreading of germination, indicating that our scenarios favoring within-individual seed size variation can be attributed to the interaction between age-dependent competition for recruitment and bet-hedging. This result also importantly highlights that bet-hedging in germination strategies is not driven *per se* by weekly rainfall variation within years, σ^2_{within}, but also by the spatial scale of rainfall variation, which affects correlations in environmental conditions experienced among individuals within populations.

(i) No priority effects lead to fixed, safe strategies. Without priority effects, i.e. all competition for recruitment is independent of seedling age, obligate dormancy evolves causing germination at the beginning of the wet season (Fig. S1, evolved values of d_μ form a flat line over a range of within-year rainfall variance σ^2_{within}). This holds even under high σ^2_{within}, for which dry-season germination and seedling survival may often be possible, because there are no competitive benefits to early germination and so even small risks are not worth taking. Accordingly, within-individual variation in dormancy period d_σ evolves values close to 0. Bet-hedging has no effect on the evolution of d_μ or d_σ in this scenario, because there is no variance in expected fitness nor fitness correlations among related individuals (Fig. S1, dots show coarse-grained and stars fine-grained environments). Such fixed strategies and absence of evolutionary conflicts of interest in the short and long term are also predicted by our density-independent phenomenological model (Fig. 1, large seeds are always favored when c=1, i.e. leftmost part of each subplot, regardless of whether arithmetic or geometric mean fitness is maximized).

(ii) Priority effects favor risky strategies and within- and among-individual variation. When adding priority effects in the form of age-dependent recruitment success, we observe both earlier germination ($d_\mu < 26$) and increased variation in dormancy ($d_\sigma > 0$). Interestingly, we often observe stable coexistence between two distinct strategies, one involving earlier but less variable germination (low d_μ and low d_σ), and one involving later but more variable germination (higher d_μ and high d_σ). Because of this evolved genetic correlation, simple population-wide genotype averages are not informative. Fig. 3 (and supplementary figures S4 and S5) therefore shows resulting multilocus strategies in genotype space (d_μ and d_σ) from 10 replicate simulations as separate colors, with points connected by a line whenever multiple strategies coexisted until the end of the simulation. Actual distributions of germination timing for each of 5 representative replicates are shown as colored inset histograms on the right. These demonstrate that the more variable strategy (darker hued histograms) produces some seeds that germinate earlier than the less variable strategy (lighter hued histograms), with these early seeds winning the competition for recruitment in years where dry season rainfalls are favorable. In years with unfavorable ‘false’ dry season rains (followed by several weeks of no rain before the start of the wet season in week 26), the seeds of the more variable strategy germinate later on average.

Because some simulations ended with one and others with two distinct strategies, we ran additional simulations with these parameter combinations to determine the stability of coexistence between the distinct strategies (low or high d_μ and d_σ), when either of the strategies can be lost due to e.g. demographic and environmental stochasticity. In Fig. S2 we show that each strategy is successful in invading a population consisting of individuals using the alternative strategy. This indicates that negative frequency-dependent selection favors each strategy when rare, leading to stable coexistence, and that results in e.g. Fig. 4 and S4 with only a single strategy may represent only transient losses of a strategy, after stochastic events and before sufficient mutations again generate the 'right' multilocus genotype to invade. Note that we started simulations with large variation in d_μ and d_σ. To check whether two coexisting strategies would also evolve if simulations were initiated with less variation, we ran control simulations starting with no genetic variation (Fig. S3). These confirmed that the observed coexistence evolves also in these cases, via an evolutionary branching event.

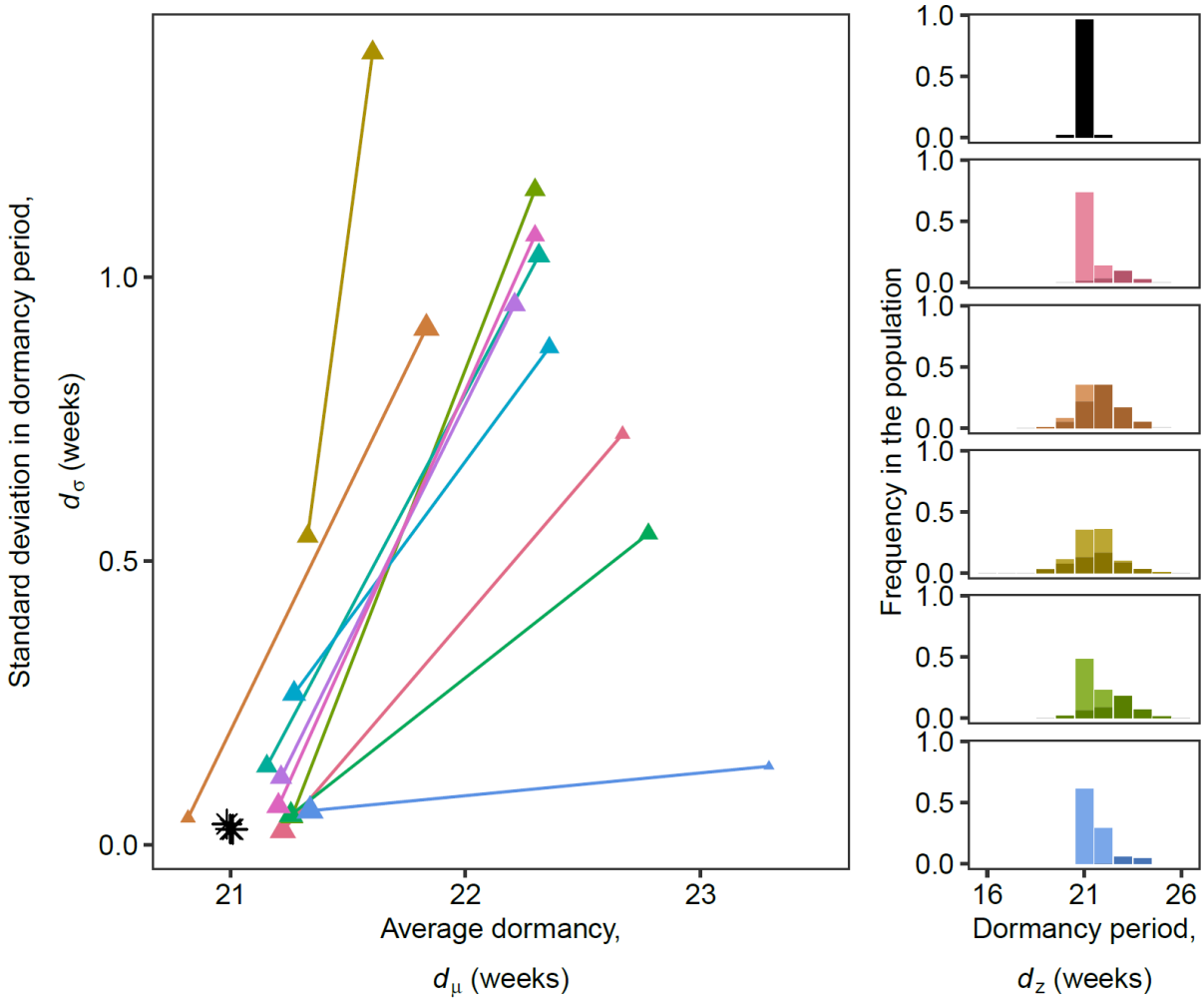

Figure 3: Left panel shows average evolved seed dormancy strategies represented by a combination of dormancy period (d_μ) and standard deviation in dormancy period (d_σ) when dry season rainfall variance $\sigma^2_{within}=2$ (see table 1 for other baseline parameter values). Each population is represented in trait space by two colored triangles connected by a solid line if two strategies coexisted in the population at the end of the simulation, with triangle sizes proportional to the fraction of the population using each strategy. The black stars represent populations in fine-grained environments (that always evolved a single strategy). Histograms on the right shows the distributions of the actual dormancy periods produced by the genotypes in the population. Histogram colors correspond to point color in the left panel. For simulations with two coexisting strategies the distribution of dormancy periods is plotted in a darker hue for the strategy with higher d_σ.

We also note that under a fine-grained rainfall pattern (black star and histogram in Fig. 3), no variation in dormancy evolves within individuals (d_σ remains low) nor among individuals (two distinct strategies never occur). Although age-dependent competition for recruitment now favors earlier germination than occurred without priority effects ($d_\mu < 26$), this competitive pressure does not result in variable germination timing. Thus, we identify both within- and among-individual variation in seed dormancy as resulting from an interaction between bet-hedging in coarse-grained variable environments, priority effects due to age-dependent seedling competition, and negative frequency-dependent selection.

(iii) Only intermediate mortality risks select for mixed strategies. Because seedling mortality strongly affects the risks of early germination, any variation in germination timing occurs at intermediate levels of mortality risk in the dry season. In the scenario illustrated in Fig. 4A we adjust the parameter a_{infl}, the inflection point of the survival function, i.e. the age at which survival rises steepest, such that higher (later) a_{infl} entails higher overall mortality (see Fig. 2). We find that low mortality (blue results in Fig. 4A) always selects for germinating as soon as possible (because of priority effects), i.e. $d_\mu = 0$ and $d_\sigma = 0$. On the other hand, very high mortality (due to high a_{infl}; black results in Fig. 4A) always selects for germinating right at the start of the wet season ($d_\mu = 26$ and $d_\sigma = 0$). Thus, only intermediate mortality risks (Fig. 3) favor variable dormancy periods. Again, this general result corresponds well with our phenomenological model (Fig. 1).

(iv) Low adult mortality increases the strength of priority effects. A final observation in this model is that, in contrast to traditional predictions from bet-hedging theory, longer lifespans select for increased spreading of germination. This effect arises because of our implementation of density-dependence, where lower adult mortality means that fewer 'slots' are opened up every year for seedlings to recruit into. This increases the intensity of age-dependent competition, which leads to stronger selection for early germination the higher the

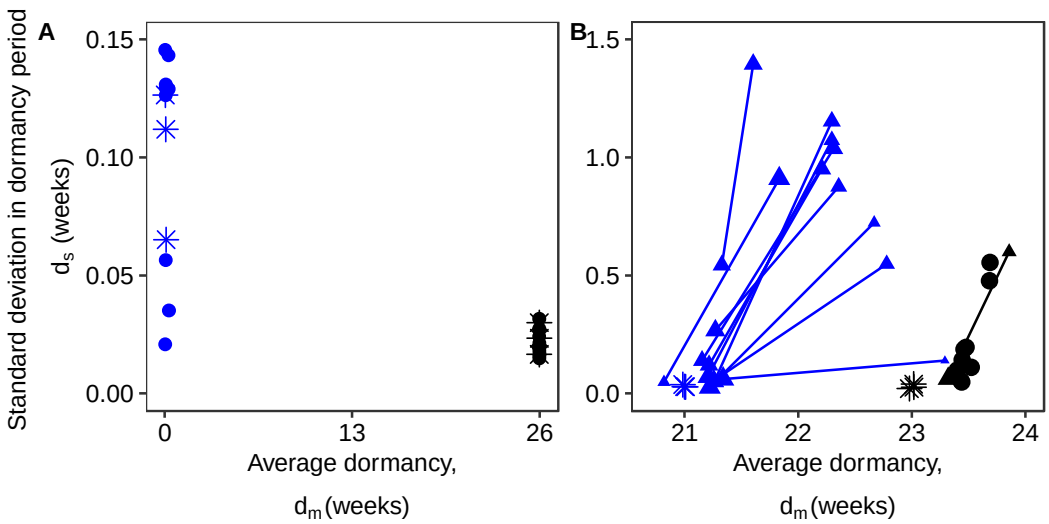

Fig. 4 Average evolved seed dormancy strategies combining dormancy period (d_μ) and standard deviation in dormancy period (d_σ) when dry season rainfall variance $\sigma^2_{\text{within}}=2$ (See table 1 for other baseline parameter values). Each population is represented in trait space by one point if exhibiting a single strategy at the end of the simulation (circle), or two points if two strategies coexisted in the population at the end of the simulation (triangles connected by a solid line), with point sizes proportional to the fraction of the population using each strategy. Stars represent populations in fine-grained environments (always evolving a single strategy). A: Results for different seedling survival (Blue: Low, $a_{\text{infl}} = 0$; Black: High, $a_{\text{infl}} = 16$). B: Results for different adult mortality (Blue: Low, $S_{\text{adult}} = 0.997$; Black: high $S_{\text{adult}} = 0.994$).

adult mortality (Fig. 4B, results shown for high adult mortality, in black, and low adult mortality, in blue). As above, this can lead to coexistence of two different strategies: an early germinating, low-variance strategy (low d_μ and low d_σ), and a later germinating, high-variance strategy (higher d_μ and high d_σ). For both low and high adult mortality, removing any effects of bet-hedging by implementing fine-grained rainfall patterns leads to populations with only a single, fixed strategy of even shorter dormancy periods. Thus, both among- and within-individual variation in germination timing increases due to combinations of life-history, bet-hedging and intensity of intraspecific competition.

Discussion

Modelling results and insights

Our two complementary modelling approaches have shown how stochastic seasonal environments can select for within- and among-individual variation in germination behavior through interactions between bet-hedging, priority effects due to age-dependent seedling recruitment, and negative frequency-dependent selection. First, our numerical model considering discrete variation ("small" early-germinating vs. "large" late-germinating seeds) reveals ample scope for bet-hedging in a density-independent setting, where long-term geometric growth rates are often highest for populations producing a mixture of the two seed types, whereas arithmetic growth rate is always maximized by producing a single seed type. This model revealed that the two key parameters selecting for seed size variation were those that affect the relative strength of fitness differences among years for the two seed types: the strength of priority effects (competitive advantage to early-germinating small seeds) and the riskiness of early germination (seedling mortality, probability of 'false rains').

Inspired by these results, we next built an evolutionary simulation model of dormancy period, where we included density-dependence as well as continuous within- and among-individual variation in seed size. To do so, we allowed the genotype's mean and variation in dormancy period to evolve independently. We identified the evolution of two distinct germination strategies. One strategy involved the production of seeds with short dormancy periods and low variance in dormancy duration, and the other involved the production of seeds with longer dormancy periods with higher variance in dormancy duration. This second strategy produces high-risk high-reward early germinating seedlings that are competitively superior in years when dry-season rains are sufficient to ensure seedling survival until the start of the wet season. In addition, this strategy also produces late-germinating seedlings that survive (but may suffer a competitive disadvantage) if false rains killed their earlier-germinating siblings. Through comparisons with evolutionary outcomes in fine-grained environments, which did not exhibit this variable strategy, we conclude that this represents a diversifying bet-hedging strategy, where the fitness returns of offspring are decoupled, thus ensuring low genotype-level variance in fitness (Starrfelt and Kokko 2012). Interestingly, negative frequency-dependent selection often led to stable coexistence of these two strategies within populations (Fig. S2), even in simulations initialized without standing genetic variation (via an evolutionary branching event, see Fig. S3).

The stable coexistence of such distinct germination strategies due to negative frequency-dependence has rarely been discussed in the bet-hedging literature (but see Gourbière and Menu 2009). While it is well-known empirically and theoretically that different mechanisms for coping with uncertainty cancel each other out, in the sense that the existence of one risk-reducing mechanism reduces the need for another (Venable and Brown 1988; Gerber and Kokko 2018; Haaland et al. 2020) (but see Snyder 2006), little is known about when each of them would be more favored. In specific modeling scenarios one strategy will typically have the advantage over the other, and many studies have looked at optimal or evolutionarily stable combinations of conservative and diversifying bet-hedging (Olofsson et al. 2009; Franch-Gras et al. 2017), or the factors shifting the balance among the two (Einum and Fleming 2004; Crowley et al. 2016). As opposed to simple comparisons of the long-term fitness of the different strategies, the flexible setup of our density-dependent simulation model allowed us to identify negative frequency-dependent selection maintaining both strategies within a population.

Our work demonstrates that explicit consideration of density-dependence in necessary for understanding the adaptive value of both within- and among-individual variation in offspring phenotype in long-lived organisms. Variation in offspring size both within and among individuals is not only common in perennial plants, but also in many other iteroparous organisms including arthropods (Fox and Czesak 2000), birds (Amundsen and Slagsvold 1998), fish (Einum and Fleming 2004), and marine invertebrates (Marshall and Keough 2007). While among-population variation is often interpreted as adaptive, within-individual variation, on the other hand, is mostly viewed as maladaptive (Fox and Czesak 2000). This interpretation is possibly driven by the focus on optimality models (e.g. Smith and Fretwell 1974; Einum and Fleming 2004), which by definition predict a single offspring size to maximize fitness (Metz et al. 2008). Approaches that take frequency-dependent interactions into account, however, show that within-individual variation in offspring size can be adaptive, even in the absence of environmental unpredictability (e.g. Geritz 1995). Our work shows that such an ecological approach is also necessary to understand evolution in unpredictable environments.

Germination strategies in seasonal environments

Our models were inspired by the wet-dry seasonal dynamics characterizing large parts of the tropics (Feng et al. 2013). Yearly patterns of seedling emergence such as those described by Garwood (1983) for Barro Colorado Island in Panamá suggest that germination during the early part of the rainy season predominates, although there is considerable variation (see also Escobar et al. 2018). Garwood's study also hinted at an important role of priority effects in that seedling emergence in highly competitive light gaps tended to occur earlier than did emergence in less competitive understory habitats. Our models provide a mechanistic explanation for these patterns, and also suggest that ongoing changes in the predictability and temporal variation in precipitation patterns in the tropics may select for altered germination strategies in tropical plants (Feng et al. 2013).

The adaptive challenges faced by plants of seasonal tropical forests are in some ways analogous to those of arctic-alpine plants facing the problem of 'false springs' followed by freezing events, which is thought to select for dormancy or other mechanisms to avoid

detrimental fitness effects of premature germination (Schwienbacher et al. 2011; Mondoni et al. 2012). Arguing that within-individual variation in germination timing could be beneficial as a bet-hedging trait, Simons & Johnston (1997) used a model of such a system to illustrate their argument that developmental instability could be adaptive in annuals. During a time when developmental instability was largely seen as maladaptive (c.f. the debate surrounding fluctuating asymmetry), substantial work on bet-hedging strategies has largely resolved this controversy (Zhang and Hill 2005; Devaux and Lande 2010; Scheiner 2014; Tufto 2015), and the dynamics considered by Simons & Johnson (1997) are now a canonical example of bet-hedging in seasonal phenology.

A second source of inspiration for our model was the extensive variation in seed size often observed in angiosperms (Michaels et al. 1988), and the many studies reporting relationships between seed size and germination behavior (e.g. Simons and Johnston 2000; Norden et al. 2009; Martins et al. 2019). Although seed size is sometimes thought about as a highly canalized trait (because there should be an optimal balance between size and number of offspring; Smith and Fretwell 1974), both categorical (seed heteromorphism) and continuous variation in seed size is common (e.g. Susko and Lovett-Doust 2000). In a recent phylogenetic analysis, Scholl et al. (2020) analyzed the occurrence of seed heteromorphism in a large sample of the flora of southwestern North America, and detected weak associations between seed heteromorphism and several measures of environmental predictability (aridity and precipitation seasonality). While the tendency for seed heteromorphism to be more likely in more unpredictable environments is consistent with our phenomenological model, these authors explicitly excluded species with continuous variation in seed size from their analyses. Our model predicts that not only seed heteromorphism, but also continuous variation in seed size could represent a bet-hedging strategy in unpredictable environments (c.f. Simons & Johnston's (1997) suggestion of developmental instability causing adaptive variation in germination timing). Interestingly, Scholl et al. (2020) failed to detect a correlation between seed heteromorphism and the annual life cycle, contrary to their expectations from previous bet-hedging theory. Although seed heteromorphism was more common in annuals than in perennials, they attributed the lack of a detectable effect to the small overall proportion of seed-heteromorphic species. However, the common occurrence of seed heteromorphism also among perennials can further be seen as an indication that the processes interacting with bet-hedging in our model to produce variation in germination phenology may indeed be common and important in natural systems.

Empirical guidelines and predictions

Our models yield several testable predictions about the relationship between germination behavior, seed size, and environmental predictability. The simplest prediction arising from our results is that germination behavior and associated traits (e.g. seed size) can vary adaptively within populations, and possibly more so in more unpredictable environments. However, we also find that the distinctions between fine- vs. coarse-grained environmental variation, and among- vs. within-year variation, are important in driving germination patterns. This implies that caution is needed when interpreting measurements of environmental variation and using them to predict ecological gradients of germination strategies. For example, the measurement of rainfall variation used in Scholl et al. (2020) was based on among-year variation (coefficient of variation of annual rainfall measurements) and the

smallest spatial grid used was 25 km^2, both of which might explain the lack of a relationship between rainfall variation and the occurrence of seed heteromorphism. Another reason highlighted by our individual-based model could be that a variable germination strategy (diversifying bet-hedging) is not the only possible adaptation to unpredictable environments, but that alternative, less variable strategies may also occur, and sometimes coexist within populations.

Recent studies of continuous seed size variation and germination behavior in the tropical vine *Dalechampia scandens* have revealed predictable covariation between measures of environmental predictability and germination behavior. Martins et al. (2019) found that seeds from populations occupying more seasonal environments required longer periods of after-ripening (duration of storage required before germination occurs in response to favorable wet conditions) before germinating, and that within each population, smaller seeds required shorter periods of after-ripening. In a follow-up study, Pélabon et al. (2021) considered variation in seed size within individuals and detected a positive relationship between environmental stochasticity and variation in seed size. Environmental unpredictability as defined by Pélabon et al. more closely resembles our parameter σ_{within} in describing stochastic variation in rainfall patterns, and our model thus provides mechanistic support for the hypothesis that the patterns of seed size variation and germination behavior in *Dalechampia* represents a bet-hedging strategy in unpredictable environments.

While observational studies of germination timing and seed size across ecological gradients may continue to yield insights into variation in these traits, experimental studies would be highly valuable. Seed-sowing experiments with seed families of known descent would specifically allow separating environmental and genetic causes of variation, and lead to insights into the evolutionary potential of germination behavior (e.g. Simons & Johnson 2006). However, separating the presence of two distinct strategies from continuous variation may continue to prove difficult, especially when the difference in mean behavior between strategies is small, and variation around these means is large.

Limitations and caveats of the model

Our model results are consistent with empirical patterns of seed size and germination behavior, yet some caution is needed when interpreting the evolution of distinct, coexisting strategies that occurred in our individual-based model. In particular, the specific genetic architecture and simple asexual mode of inheritance we assumed might affect the ability to evolve separate strategies. These issues are not unique to our study, because any evolutionary simulation model of the kind presented here must necessarily make some assumption about the genetic architecture of the traits they model. A major assumption we made is that mean and variance of dormancy duration evolve independently, allowing us to predict the optimal combination of these traits in the absence of any constraints. Evolution of these optimal combinations may be difficult to attain due to genetic constrains, covariation with other traits, or trade-offs.

Importantly, we did not incorporate a trade-off between offspring quality and dormancy period, which could be expected if we assume that seed size is the mechanism by which variation in germination strategy is achieved (Stearns 1989). Furthermore, we did not include a cost to variation (or canalization, see Zhang and Hill 2005). However, while such additional

assumptions might affect our results (for example by narrowing the parameter space in which variable strategies are selected for if adding a cost to variation, and widening it if adding a cost to canalization), they also reduce generality and do not subtract from the general point. Variation in germination strategies may arise from other sources than simply seed size variation resulting from per-offspring parental investment (Simons and Johnston 2006; Baskin and Baskin 2014) and as with costs of variation vs. canalization, we note that the pattern may also go either way with regards to the seed size vs. germination strategy (offspring quantity vs quality) trade-off: In many species, larger seeds germinate earlier (Biere 1991; Simons and Johnston 2000; Pélabon et al. 2005), but the opposite pattern is also observed (Susko and Lovett-Doust 2000), and among species time to germination is usually longer for larger seeds (Norden et al. 2009; Harel et al. 2011). Thus, while adding some trade-off between seed set and germination strategy might increase realism with respect to certain systems, generality would again necessarily be lowered relative to our present model without such energetic constraints.

Our assumption of a simple asexual reproductive system is also not representative of the majority of plant species. Indeed, plant mating systems are highly variable, and near-complete selfing is uncommon compared to mixed and predominantly outcrossing systems (Moeller et al. 2017). Although we find evolution of two coexisting strategies when using asexual reproduction, gene flow due to random outcrossing might inhibit the emergence of two genetically distinct germination strategies. Therefore, reproductive isolation mechanisms that restrict gene flow between newly arising strategies need to evolve to restore our results in case of sexual reproduction.

In addition to dormancy, germination timing is also driven by variation in flowering and fruiting phenology as well as the duration of fruit maturation (Escobar et al. 2018). Although we chose to keep these processes fixed in our model in order to assess specifically the joint evolution of mean and variation in a single trait (seed size) affecting germination behavior, variation in flowering time additionally leads to non-random mating and is therefore an interesting trait to add in further studies.

Conclusions

This study has demonstrated novel mechanisms by which variation in germination strategies in perennial plants can evolve, shedding light on the prevalence of seed heteromorphism and continuous seed-size variation seen in perennials as well as annuals. Seed size was historically considered a highly canalized trait, to the point that the weight measurement ‘carat’ was based on the remarkably invariant seeds of the carob tree (*Ceratonia siliqua*). However, it has since been discovered that substantial variation in seed size is widespread, even in carob seeds (Turnbull et al. 2006), and its universality begs an explanation. Bet-hedging in desert annuals has previously been the best-studied empirical and theoretical example of variable germination strategies, but there are arguably more perennial species occupying seasonal tropical or temperate environments than there are desert annuals. Our modelling results, where bet-hedging in perennials interacts with unpredictable seasonal variation and competitive priority effects to produce within-individual variation in germination strategies, therefore provide a much-needed extension to existing theory on this topic. A better understanding of competitive dynamics in stochastic seasonal environments can help improve

the predictability of species and community responses to ongoing changes in climate patterns and other anthropogenic challenges.

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Author contributions:

All authors initiated the study. HtB and TRH developed and analyzed the models. HtB ran the simulations. ØHO reviewed the empirical literature. TRH reviewed the theoretical literature and drafted the manuscript with input from all authors.

Data Accessibility Statement:

All code, code output, and scripts will be made available online upon journal acceptance at Dryad, and is until then available upon request.

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Supplementary material

Part 1: Results without priority effects

In the absence of priority effects, individuals will evolve a mean germination period of about 26.5 weeks, independent of the variation in rainfall (Fig S1A). Within-individual variation in dormancy period d_σ evolves to values close to 0 (Fig S1B). We find this result in both coarse- and fine-grained environments. The evolved genotypes result in dormancy period of 26 or 27 weeks (Fig S1C).

Note that seeds will only germinate if the rainfall R_t exceeds the threshold value R_{thres}. Seeds with a dormancy period of 26 weeks, will therefore not experience a dry week, since they will only germinate in last week of the dry season if it has enough rain to trigger germination.

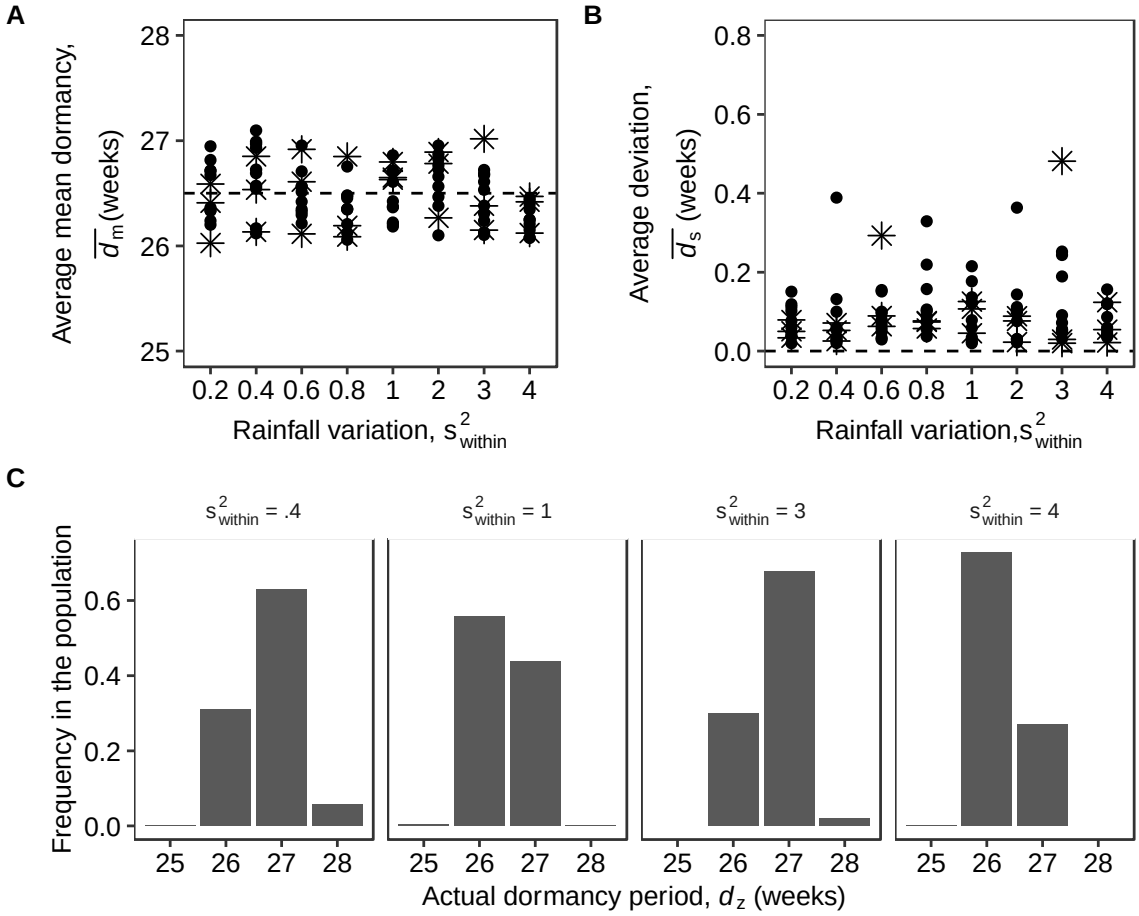

Fig S1: Mean evolved traits (panels A and B) and the resulting phenotypes in the population (panel c) after 100.000 years of evolution in the absence of priority effects over a range of values of within-year rainfall variability σ^2_{within}. Panels A and B: The dots show coarse-grained and stars fine-grained environments. In panel C, we show the resulting phenotypes for the replicate with the highest value for σ, under some of the σ^2_{within} scenarios. Parameters are as in table 1.

Part 2: Invasion dynamics and evolutionary branching

In some parameter regions, we observe alternatively a single strategy or two coexisting strategies in the population at the end of the evolutionary simulations. Here, we show that both strategies (long mean dormancy and high variation in dormancy period; short mean dormancy and no or low variation in dormancy period) have an evolutionary advantage when invading a resident population of the other strategy (Fig. S2). As a representative example, we use the genotypes that evolved in the purple replicate in Fig. 3 in the main text. Because of this negative frequency-dependence, we interpret any observations of only a single strategy being present in the population at the end of the simulation as a result of transient dynamics, e.g. that stochastic events causing the extinction of one strategy, and that the right (multilocus) mutations have not yet occurred to allow it to re-establish.

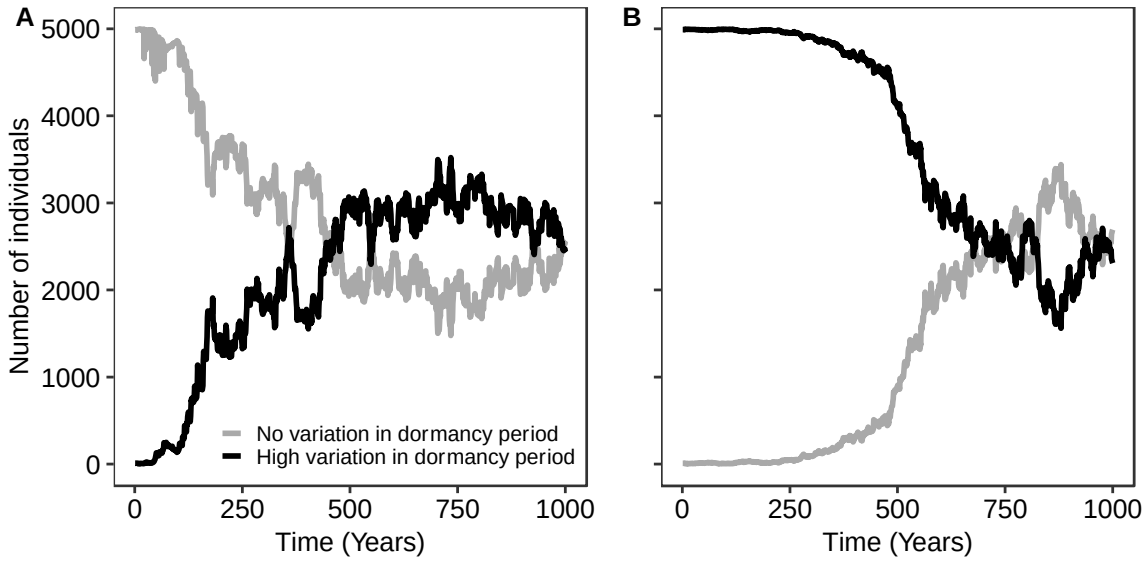

Fig S2: Ecological time series for two situations with a highly unpredictable dry season and two coexisting strategies. The black strategy produces seeds with late mean and high variation in dormancy period ~N(22.3,1.07^2); the grey strategy has seeds with short mean and low variation in dormancy period, ~N(21.2,0.07^2). These are the strategies at the end of the simulation of the purple population in Fig. 3. In the dry season the rainfall is normally distributed with ~N(0, 2), which means that the probability to get a rain-triggering event (rain ≥ 1) is ≈24%. Panel A shows ecological dynamics when the black strategy (10 individuals) invades a population where the grey strategy is resident (4990 individuals) at carrying capacity, while in panel B the grey strategy invades the black population. Default parameters otherwise (See table 1).

We also ran additional simulations initiating the populations with no genetic variation in d_μ and d_σ, in order to check whether separate strategies evolved also in this case, and not just as a consequence of initiating the populations with sufficient standing genetic variation. The resulting time series (Fig. S3) demonstrate that a single two-locus strategy evolves at first, until an evolutionary branching point is reached whereafter two separate strategies evolve and stably coexist.

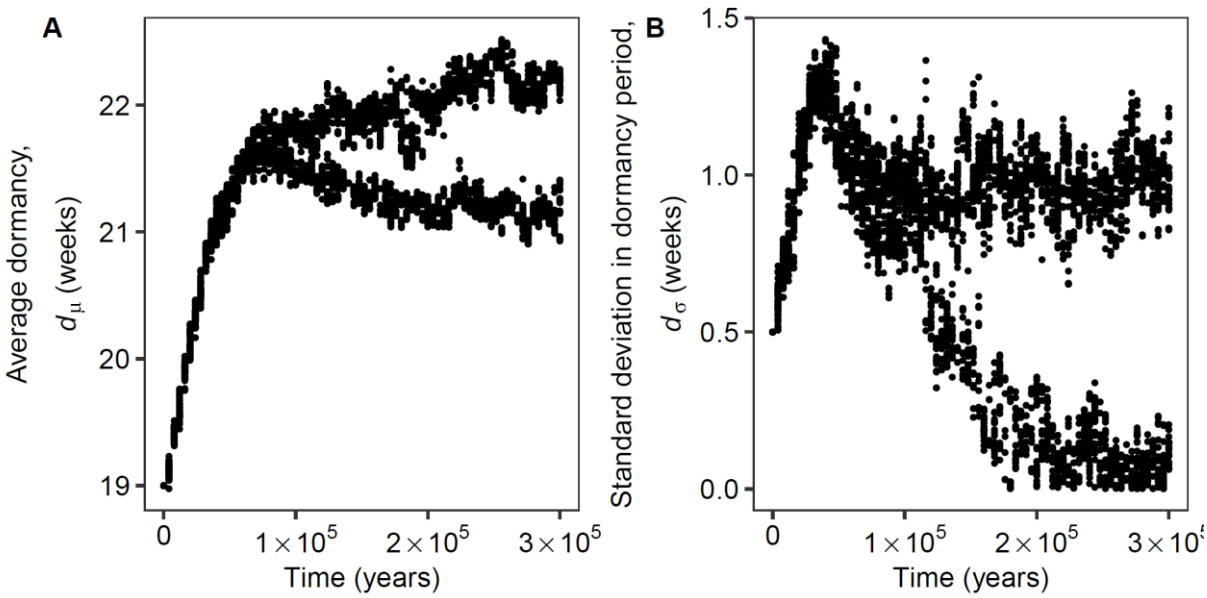

Figure S3: Evolutionary time series of the two evolving traits (mean dormancy period, d_μ, in panel A and standard deviation in dormancy period, d_σ, in panel B), when starting the simulations without any genetic variation (d_μ=19 and d_σ=0.5 for all individuals). Points represent a random subset (1%) of the individuals in the population at a given time step. Initially the population evolves a single strategy, but after an evolutionary branching point is reached the populations splits into different strategies. For computational purposes, the mutation rate for both traits was increased to a value of m = 0.1. In the dry season the rainfall is normally distributed with ~N(0, 2), default parameters were otherwise used (table 1).

Part 3: Less or more variation in rainfall

Here we present simulation results with lower (Fig. S4) or higher (Fig. S5) variation in dry season rainfall, σ^2_{within}. Comparing these results with those in Fig. 3 ($\sigma^2_{within} = 2$), we observe that lower rainfall variation (Fig. S4, $\sigma^2_{within} = 0.4$) leads to longer average dormancy d_μ, as early germination becomes more risky. Furthermore, we observe a decrease in both within-individual dormancy variation (lower d_σ), and among-individual genetic variation (fewer of the simulations end up with two coexisting strategies). In contrast, increasing rainfall variation (Fig. S5, $\sigma^2_{within} = 4$) leads to both higher d_σ and increased among-individual variation.

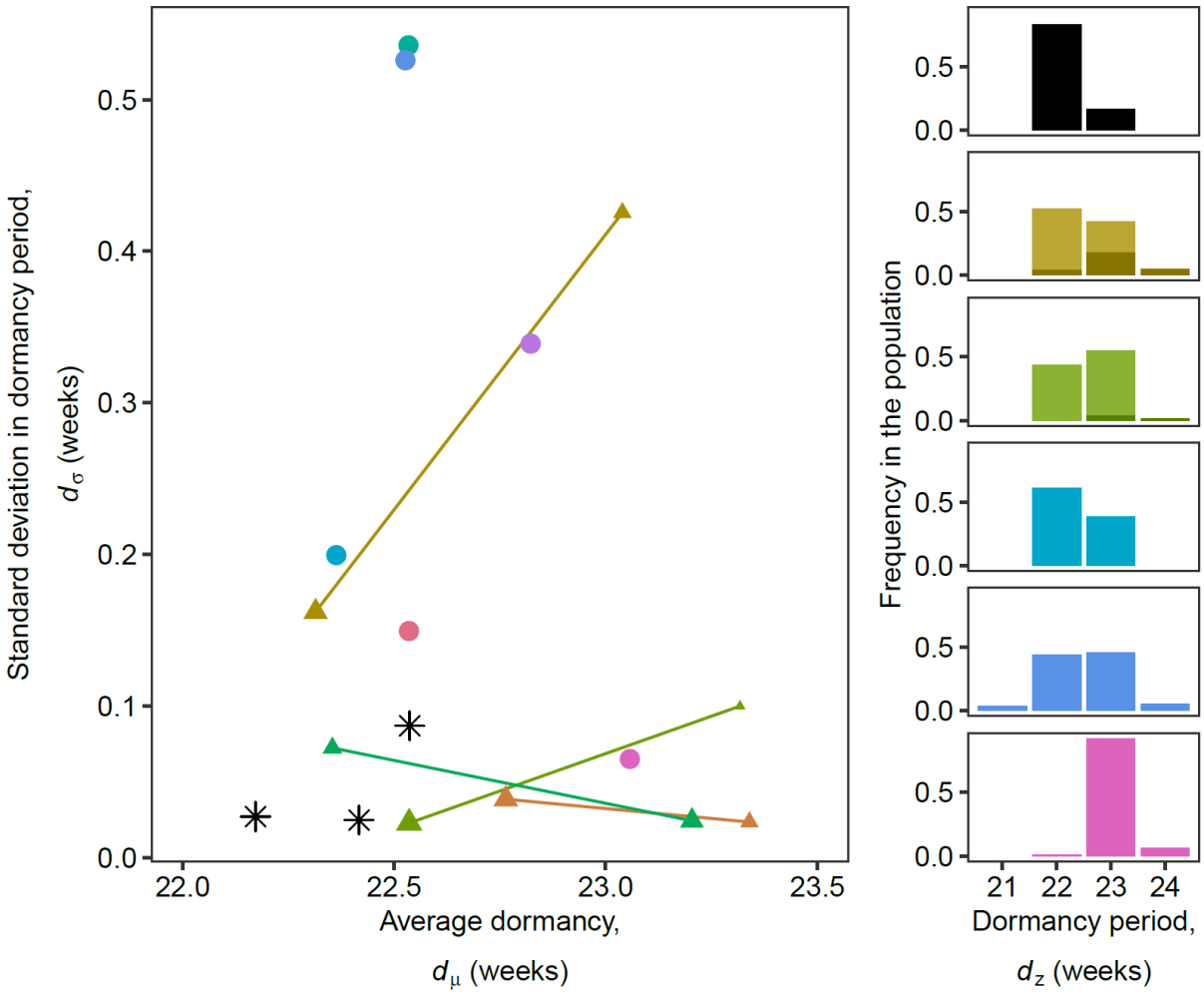

Figure S4: Left panel shows average evolved seed dormancy strategies combining dormancy period (d_μ) and standard deviation in dormancy period (d_σ) when dry season rainfall variance $\sigma^2_{within} = 0.4$. (See table 1 for other baseline parameter values.) Each population is represented in trait space by one coloured point if exhibiting a single strategy at the end of the simulation (circle), or two points if two strategies coexisted in the population at the end of the simulation (triangles connected by a solid line), with point sizes proportional to the fraction of the population using each strategy. Black stars represent populations in fine-grained environments (always evolving a single strategy). Histograms on the right shows the distributions of the actual dormancy periods dictated by the genotypes in the population. Histogram colors correspond to point color in the left panel; for simulations with two coexisting strategies the distribution of dormancy periods is plotted in a darker hue for the strategy with higher d_σ.

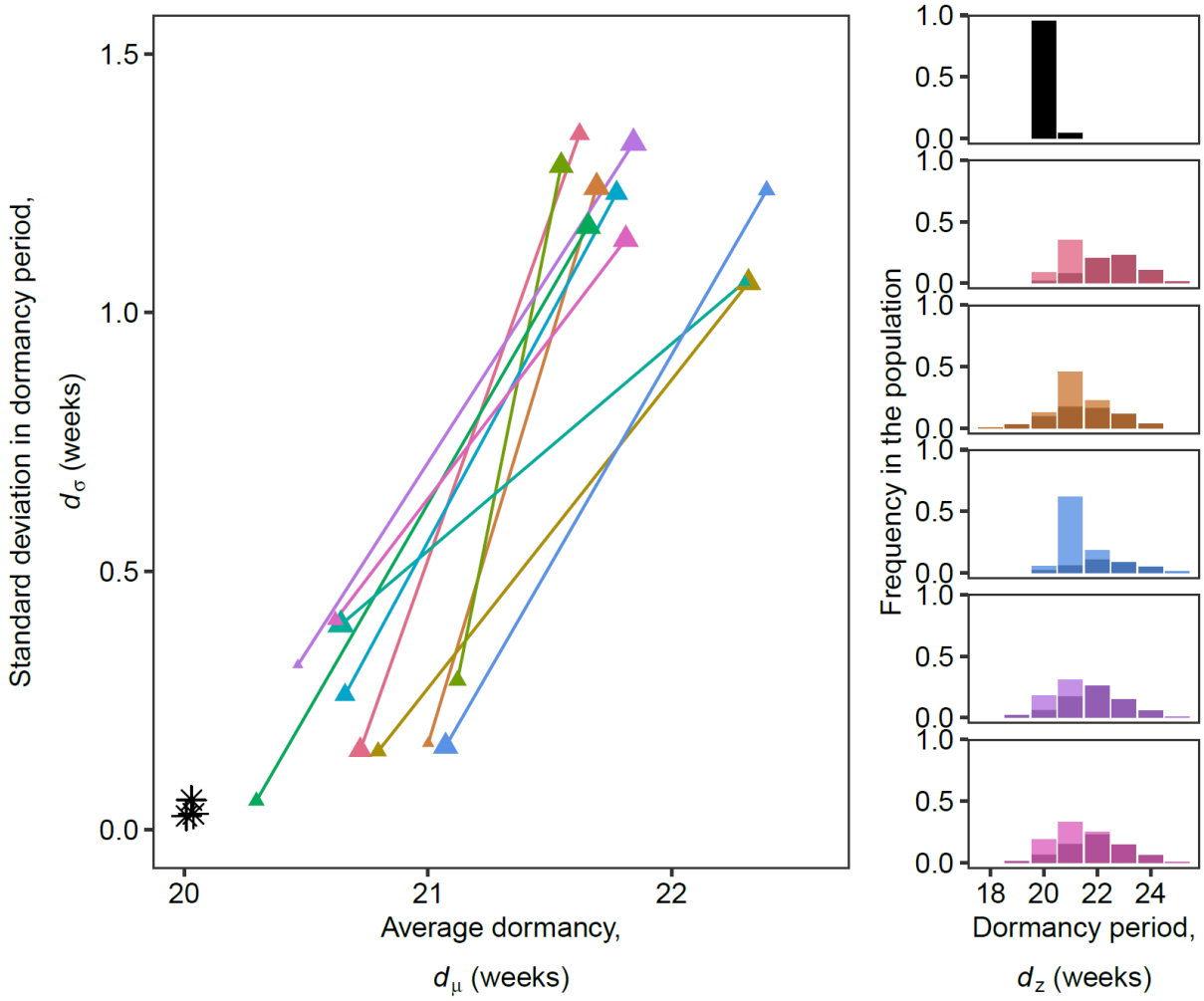

Figure S5: Left panel shows average evolved seed dormancy strategies combining dormancy period (d_μ) and standard deviation in dormancy period (d_σ) when dry season rainfall variance σ^2_{within}=4. (See table 1 for other baseline parameter values.) Each population is represented in trait space by two triangles connected by a solid line if two strategies coexisted in the population at the end of the simulation, with triangle sizes proportional to the fraction of the population using each strategy. Black stars represent populations in fine-grained environments (always evolving a single strategy). Histograms on the right shows the distributions of the actual dormancy periods dictated by the genotypes in the population. Histogram colors correspond to point color in the left panel; for simulations with two coexisting strategies the distribution of dormancy periods is plotted in a darker hue for the strategy with higher d_σ.