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A continuum of biological adaptations to environmental fluctuation

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Bet-hedging—a strategy that reduces fitness variance at the expense of lower mean fitness among different generations—is thought to evolve as a biological adaptation to environmental unpredictability. Despite widespread use of the bet-hedging concept, most theoretical treatments have largely made unrealistic demographic assumptions, such as non-overlapping generations and fixed or infinite population sizes. Here, we extend the concept to consider overlapping generations by defining bet-hedging as a strategy with lower variance and mean per capita growth rate across different environments. We also define an opposing strategy—the rising-tide—that has higher mean but also higher variance in per capita growth. These alternative strategies lie along a continuum of biological adaptations to environmental fluctuation. Using stochastic Lotka–Volterra models to explore the evolution of the rising-tide versus bet-hedging strategies, we show that both the mean environmental conditions and the temporal scales of their fluctuations, as well as whether population dynamics are discrete or continuous, are crucial in shaping the type of strategy that evolves in fluctuating environments. Our model demonstrates that there are likely to be a wide range of ways that organisms with overlapping generations respond to environmental unpredictability beyond the classic bet-hedging concept.

1. Introduction

Temporal fluctuation of environmental conditions is a universal feature in nearly every ecosystem on Earth [1,2]. In fluctuating environments where the intensity and direction of natural selection are likely to vary unpredictably over time [3–5], organisms have adopted a wide range of evolutionary strategies to maximize long-term fitness of populations [6]. Theoretical studies have long shown that both the mean and variance of fitness are critical in driving biological adaptation. Although many biological adaptations increase mean fitness while also decreasing fitness variation in fluctuating environments [7,8], there are also favoured traits that reduce the mean. To understand these types of seemingly counterintuitive strategies, a great deal of theoretical work has focused on evolutionary bet-hedging [1,9,10], which reduces variance in fitness at the expense of a lower mean. Empirically, many known biological adaptations to environmental fluctuation—as diverse as seed production in annual plants [11], phenotypic polymorphisms in bacteria [12,13] and altruistic behaviour in social animals [14]—are considered to be forms of bet-hedging. There are two general types of bet-hedging: conservative bet-hedging describes a consistent but low risk phenotype within a genotype, whereas diversified bet-hedging depicts the case when a genotype produces diverse phenotypes to reduce fitness variance [9,15,16]. Under either bet-hedging scenario, based on the concept of the geometric mean of fitness, either fitness variance minimization or the arithmetic mean fitness maximization (or both) will be favoured by natural selection [10].

In contrast with bet-hedging strategies, other forms of biological adaptation may be favoured under some forms of environmental fluctuation, despite leading

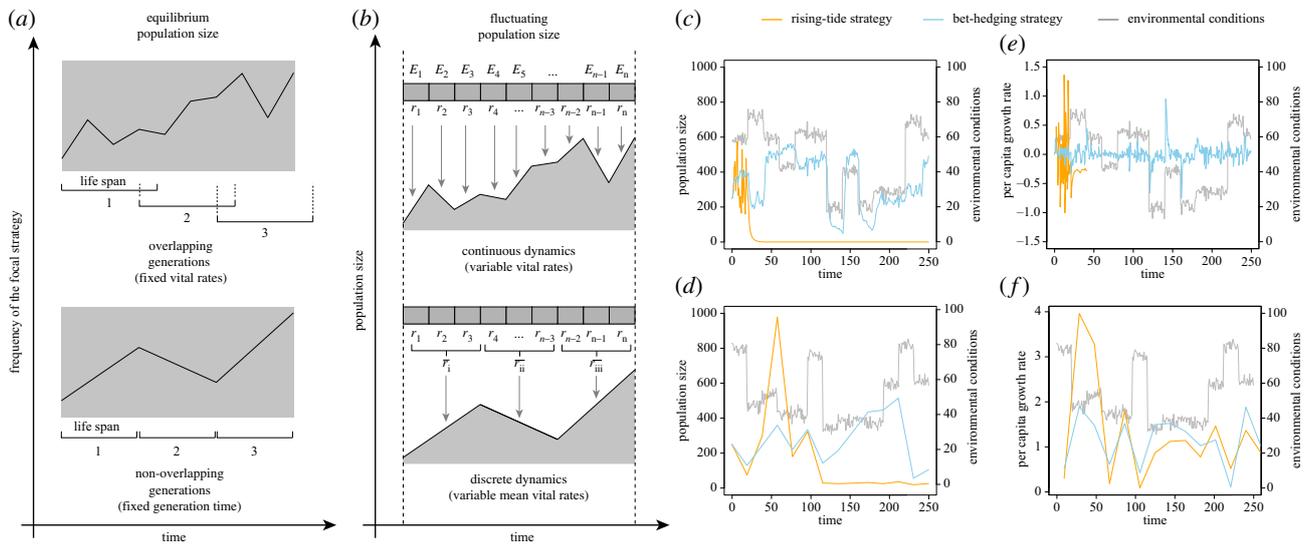


Figure 1. A schematic comparison of the demographic settings used in different bet-hedging models. (a) Many existing models either consider biological systems near an equilibrium state or largely ignore changes in population size, which is represented by the grey rectangles showing that population size remains largely constant through time. These models often focus on dynamics in terms of frequencies or the proportions of different strategies, such as whether one strategy is invading or prevailing within the population. Although the frequencies can vary, one crucial parameter—the extent of generational overlap—is often assumed to be fixed. That is, some models assume mortality in the previous generation, which creates a constant degree of generational overlap, whereas other models assume non-overlapping generations in which all parents simultaneously die as offspring mature (generations are labelled in numbers). (b) An alternative approach to modelling evolutionary processes is through selection dynamics under fluctuating population sizes. These types of models allow population size to rise and fall in response to environmental conditions. Although these models often assume variable degrees of generational overlap, something that is more applicable to most organisms, they can show more ‘non-overlapping’ characteristics under discrete-time population dynamics. (c–f) For example, while continuous dynamics let populations react to every change in environmental state (c), discrete dynamics take the temporal average fitness response before calculating the change in population size (d). Per capita growth rate, one measure of fitness, shows similar distinctions under both types of dynamic models where (e) continuous dynamics act instantly and (f) discrete dynamics calculate the average of a period of time. (Online version in colour.)

to high variance in fitness across environments. For example, studies exploring thermal niche evolution at different temporal scales of environmental fluctuation have demonstrated that although greater long-term environmental variation (e.g. seasonal variation in temperature) favours the evolution of thermal generalists, short-term variation (e.g. daily temperature variation) has an opposite effect by selecting for thermal specialists [17,18]. In other words, a specialist strategy adapted to short-term environmental fluctuation—which differs fundamentally from a bet-hedging strategy—can be shown to be more advantageous than a generalist strategy by using the approximation for geometric mean fitness, which increases with higher arithmetic mean fitness and lower fitness variance [19–21]. Essentially, these empirical results hint at the theoretical possibility that the temporal scale of environmental variation might play a critical yet largely unexplored role in shaping biological adaptation to fluctuating environments.

Most published studies on biological adaptation to fluctuating environments (e.g. [1,9,10,15,22]) are based on the geometric mean of fitness, which assumes that the fitness consequences of environmental variation within a generation are additive within an organism’s lifetime, but multiplicative across generations [23–25]. However, the concept of geometric mean fitness relies on the restrictive assumptions of (1) non-overlapping generations and (2) externally set fixed or infinite population sizes (figure 1a), both of which do not apply to many prokaryotic and most eukaryotic species [26]. In fact, fluctuation in population size—which when environmentally driven is analogous to a population going through a bottleneck in low quality environments and an expansion in high quality environments [27]—can have substantial effects on the strength and direction of selection in populations of

externally set finite size [28]. Moreover, the assumption of non-overlapping generations—which is typically used in most models of this sort (e.g. the grain-size model [22])—creates a distinction between within- and among-generation selection and only applies to a very limited number of real-world organisms, such as some microbes and annual plants that do not produce a seed bank [14,29]. Indeed, theoretical studies have shown that the geometric mean is not what natural selection maximizes in the case of density-dependent selection and variable population sizes [16,30]. Previous studies have demonstrated that, in contrast with the non-overlapping generation setting, fluctuating selection can lead to the coexistence of polymorphic strategies that are inconsistent with the bet-hedging strategy in an overlapping generation setting [31]. However, the properties of these other strategies that are selected for in an overlapping generation setting are mostly derived from the assumption of relatively small variation in population size [31–33]. Since environmentally induced changes in birth and death rates may greatly alter population size and the level of generational overlap, identifying general rules of biological adaptation to environmental fluctuation—particularly for species with overlapping generations and finite population sizes—remain elusive.

To achieve a more comprehensive understanding of biological adaptation to environmental fluctuation that applies to organisms without having to evoke restrictive demographic assumptions that are biologically unrealistic for most animal species, we use stochastic Lotka–Volterra models to examine the impact of differential selective forces with varying population sizes, different temporal scales of environmental fluctuation (electronic supplementary material, figure S1) and distinctive temporal patterns of population dynamics

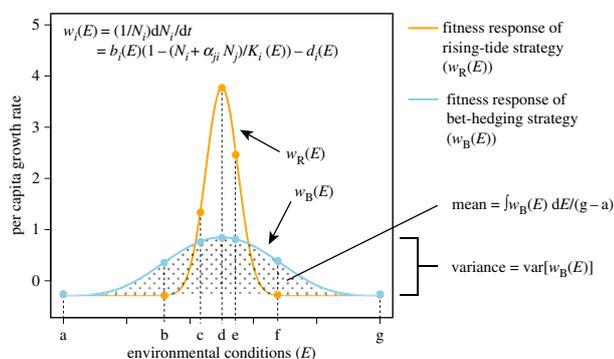


Figure 2. Definitions of the bet-hedging and rising-tide strategies in the overlapping generation model. The average fitness across all environments can be obtained by integrating the performance curve across the environmental condition axis, whereas variance in fitness can be calculated as the variance of the performance curve along the environmental condition axis. Thus, we expand the definition of bet-hedging to be a strategy with lower variance at the cost of lower average fitness along an environmental gradient. Similarly, the rising-tide strategy can be defined as a strategy with higher variance and a higher mean. (Online version in colour.)

(figure 1). We use a competitive Lotka–Volterra model as our basic framework for exploring a range of biological adaptations to fluctuating environments because this approach restricts population size through competition, rather than externally setting an absolute boundary on population size. In other words, population size is dynamically regulated by the fitness of each strategy, which in turn is affected by environmental conditions and population size itself. Moreover, Lotka–Volterra models can be used to explore natural selection, as in the case of Moran models that incorporate birth and death processes [34], without the unrealistic assumption of a fixed population size [35]. We also compare our continuous-time population dynamics model to one that uses discrete-time population dynamics to approximate the commonly used but less realistic non-overlapping generations models (e.g. [1,9,15,22]; figure 1). In addition, we use Gillespie’s algorithm [35,36] to explore the effects of demographic stochasticity in finite populations to more broadly test the generality of our model (see electronic supplementary material). Fundamentally, our model always allows for competition to reduce population size, yet the direction of selection may not be the same at each moment because environmental conditions fluctuate (i.e. we explicitly model fluctuating selection).

We begin by exploring the selection dynamics of a bet-hedging strategy that has lower fitness variation, represented by variance in the per capita population growth rate, across all environmental conditions, as well as what we call the ‘rising-tide strategy’, which has higher fitness than the bet-hedging strategy under benign conditions, but lower fitness than the bet-hedging strategy under harsh conditions (figure 2). We refer to this strategy as the ‘rising tide’ because, since it performs well under benign environmental conditions, its numbers within the population can increase rapidly, just like the rise of the tide. To represent the lower mean fitness criteria of the bet-hedging strategy relative to the rising-tide strategy, we assume that there is a smaller total area beneath the performance curve of the bet-hedging strategy than the rising-tide strategy (figure 2). Importantly, the bet-hedging and rising-tide strategies are defined relatively such that bet-hedging represents a strategy with lower mean and variance in fitness compared to a rising-tide strategy. In other words, the bet-hedging and rising-tide

strategies lie along a continuum of biological adaptations to environmental fluctuation that differ only in their degree of specialization to benign environments, which ultimately leads to different fitness variances in fluctuating environments. In many ways, the rising-tide strategy is analogous to a specialist strategy (i.e. specialized to benign conditions in fluctuating environments), whereas the bet-hedging is similar to a generalist strategy (i.e. adapted to both benign and harsh conditions in fluctuating environments). However, while the generalist strategy does not necessarily need to have a lower mean fitness than a specialist in a classic generalist–specialist framework [18], bet-hedging is defined as a strategy with lower mean fitness and lower variance in fitness than the rising-tide strategy.

2. An environment-dependent competitive Lotka–Volterra model

To investigate how different temporal scales of environmental fluctuation—often referred to as the grain of the environmental variation (*sensu* [10])—influence the evolution of the bet-hedging and rising-tide strategies, we employ continuous versions of the two strategies (figure 2; see electronic supplementary material, §S1 for additional combinations of strategies). We allow the values of the environmental conditions E to vary continuously—just as temperature and rainfall do in nature—and influence the intrinsic growth rate $b(E)$, environment-dependent death rate $d(E)$ and carrying capacity $K(E)$ of each strategy (see equation 2.2). Thus, we build a continuous-time model with probabilistic environmental settings. We also employ fast Fourier transformation (FFT) for easy visualization and quantification of the patterns of short- and long-term environmental variation (electronic supplementary material, figure S1b–g). The dynamics of the rising-tide, dN_R/dt , and bet-hedging strategies, dN_B/dt , in the stochastic Lotka–Volterra competitive model are

$$\frac{dN_R}{dt} = b_R(E)N_R \left(1 - \frac{N_R}{K_R(E)} - \frac{\alpha_{BR}N_B}{K_R(E)} \right) - d_R(E)N_R \quad (2.1a)$$

and

$$\frac{dN_B}{dt} = b_B(E)N_B \left(1 - \frac{\alpha_{RB}N_R}{K_B(E)} - \frac{N_B}{K_B(E)} \right) - d_B(E)N_B, \quad (2.1b)$$

where the capital subscripts R and B represent the parameters for the *rising-tide* and *bet-hedging* strategies, respectively. We also provide a simplified version of the model to explore the role of temporal and demographic stochasticity (electronic supplementary material, §4).

(a) A continuous-time population dynamics model

We first derive the continuous-time population dynamics model (equation (2.1)) by employing the concept of biological performance curves [37]. Specifically, the carrying capacity of a strategy (i , represented by R : rising-tide or B : bet-hedging) contains a beta probability distribution function (hereafter referred to as beta function) $f_{\text{beta}}(x; \alpha, \beta)$ and several coefficients,

$$K_i(E) = c_K \gamma_i f_{\text{beta}} \left(\frac{E}{c_{\text{range}}} ; s_i, s_i \right) = c_K \gamma_i \frac{(E/c_{\text{range}})^{s_i-1} (1 - E/c_{\text{range}})^{s_i c_{\text{sk}}-1}}{(\Gamma(s_i)\Gamma(s_i))/(\Gamma(s_i + s_i))}, \quad (2.2a)$$

where the shape parameters (s) determine the width and height of each performance curve, E stands for environmental conditions and Γ denotes the gamma function ($\Gamma(n) = (n-1)!$). In addition, two coefficients describe the interaction of performance curves and the environment: the range of responsive environmental conditions (c_{range}) and the amplitude of those responses (c_K). Lastly, the scaling coefficient for each strategy (γ_i) allows the bet-hedging strategy to have a smaller area beneath its performance curve than the rising-tide strategy (i.e. smaller average fitness). We chose to use a beta function to describe each performance curve because a beta function retains the response in finite and constant regions with boundaries (see electronic supplementary material, table S1, for details of each parameter), whereas in the more commonly used Gaussian distribution function, environmental conditions range from positive infinity to negative infinity. However, using a Gaussian distribution function in our model produces qualitatively similar results (electronic supplementary material, §3).

The intrinsic growth rate and environment-dependent death rate also follow beta functions with primarily the same parameters described above, though with different amplitudes (c_b and c_d),

$$b_i(E) = c_b \gamma_i f_{\text{beta}}\left(\frac{E}{c_{\text{range}}}; s_i, s_i\right) \quad (2.2b)$$

and

$$d_i(E) = c_d \left(d_{\text{max}} - \gamma_i f_{\text{beta}}\left(\frac{E}{c_{\text{range}}}; s_i, s_i\right) \right). \quad (2.2c)$$

Note that the death rate generates opposite responses to the environmental conditions: $K_i(E)$ and $b_i(E)$ are maximized at $E = c_{\text{range}}/2$, but the death rate is minimized under such conditions. We set this rate as the maximal response of the beta function of the rising-tide strategy ($d_{\text{max}} = f_{\text{beta}}(1/2; s_R, s_R)$) minus the current response of the beta function. We also add an additional death rate to let the environment regulate population size more directly than through density dependence. In short, changes in environmental conditions (e.g. temperature or precipitation) influence the growth rate, carrying capacity and death rate. Through these environmentally influenced parameters, each strategy can increase in population size under favourable conditions and decrease in population size under unfavourable conditions or through density regulation. To test the generality of our model, we further independently varied the population growth rate, death rate and carrying capacity as a function of changing environmental conditions, all of which produced qualitatively similar results (see electronic supplementary material, §S2).

The above section dealt with biological responses to different environmental conditions. Now let us explain how the environment changes in the model. Although we consider different time scales of environmental variation by modelling both short- and long-term variation, we recognize that natural environmental variation could have other components, something to be modelled in future studies. We assume that the two scales of environmental variation (E_{long} and E_{short}) vary within constant ranges (c_{long} and c_{short}) and follow beta distributions with given sizes of variation:

$$\frac{E_{\text{long}}}{c_{\text{long}}} \sim \text{beta}(s_{\text{long}}, s_{\text{long}}) \quad (2.3a)$$

and

$$\frac{E_{\text{short}}}{c_{\text{short}}} \sim \text{beta}(s_{\text{short}}, s_{\text{short}}), \quad (2.3b)$$

where $\text{beta}(s_{\text{long}}, s_{\text{long}})$ and $\text{beta}(s_{\text{short}}, s_{\text{short}})$ represent beta distributions with shape parameters, s_{long} and s_{short} , respectively.

The short-term environmental variation (E_{short}) is resampled in each time unit, whereas the long-term variation (E_{long}) is resampled once in m time units. The current environmental condition (E) is the sum of the deviations of the two sampled environmental variations:

$$E = E_{\text{mean}} + E_{\text{long}} - \frac{c_{\text{long}}}{2} + E_{\text{short}} - \frac{c_{\text{short}}}{2}, \quad (2.4)$$

where the mean of the two distributions is in the middle of the environmental ranges (i.e. $c_{\text{long}}/2$ and $c_{\text{short}}/2$), since both distributions are symmetrical. We validated the behaviour of the environmental fluctuations through fast Fourier transformation (electronic supplementary material, figure S1).

(b) The discrete-time population dynamics model

Based on the continuous-time population dynamics model described above, we then derive the discrete-time population dynamics model. Instead of changing parameters instantly according to changes in the environment (e.g. $b_i(E)$), the discrete model takes the arithmetic mean from several (m) environmental inputs before calculating changes in population dynamics. The parameters include

$$\bar{K}_i = \sum_{j=1}^m K_i \frac{E_j}{m}, \quad (2.5a)$$

$$\bar{b}_i = \sum_{j=1}^m b_i \frac{E_j}{m} \quad (2.5b)$$

$$\text{and } \bar{d}_i = \sum_{j=1}^m d_i \frac{E_j}{m}, \quad (2.5c)$$

where i specifies the strategy and j denotes the index of environmental condition. Hence, the population dynamics follow

$$N_{R,t+1} = N_{R,t} + \bar{b}_R N_{R,t} \left(1 - \frac{N_{R,t}}{\bar{K}_R} - \frac{\alpha_{BR} N_{B,t}}{\bar{K}_R} \right) - \bar{d}_R N_{R,t} \quad (2.6a)$$

and

$$N_{B,t+1} = N_{B,t} + \bar{b}_B N_{B,t} \left(1 - \frac{\alpha_{RB} N_{B,t}}{\bar{K}_B} - \frac{N_{B,t}}{\bar{K}_B} \right) - \bar{d}_B N_{B,t}, \quad (2.6b)$$

where t stands for the index of calculations. Note that each calculation is based on the average of m environmental conditions. Because the environment resamples in the same way as the continuous-time population dynamics model, each calculation has one sample of long-term variation and m samples of short-term variation. Thus, the long-term environmental variation represents among-calculation variation and the short-term environmental variation represents within-calculation variation in the discrete-time population dynamics model (figure 1d–f). We set this to approximate the within- or among-generation variation design in most common bet-hedging models [9,10,15].

3. Results

We find that the effect of different temporal scales of environmental fluctuation on the evolutionary outcome strongly

depends upon whether the mean environmental conditions match the optima of the performance curves. When the mean condition is at the optimum of the performance curves of the rising-tide and bet-hedging strategies (figures 3a–g and 4a), it is common for the rising-tide strategy to exclude the bet-hedging strategy (figure 4d). Yet, larger long-term environmental variation favours the bet-hedging strategy (figures 3a,d,e and 4g), whereas greater short-term environmental variation leads to the coexistence of the bet-hedging and rising-tide strategies (i.e. a polymorphism of strategies) (figures 3a–c and 4j).

Next, we show that if the mean environmental condition deviates from the optimum of both strategies (figures 3h–m and 4c), environmental variation can have complex and counterintuitive effects on adaptive evolutionary responses. Since the rising-tide strategy is more specialized to the optimal environment, the bet-hedging strategy dominates when both long- and short-term environmental variation are low (figures 3h and 4i). Interestingly, if long-term variation increases, the rising-tide strategy sometimes excludes the bet-hedging strategy (figures 3h,k,l and 4f). Similarly, the rising-tide strategy coexists with the bet-hedging strategy when there is higher short-term environmental variation (figures 3h–j and 4l). When both short- and long-term environmental variation are relatively high, the bet-hedging strategy again becomes more dominant (figure 4i). In other words, increasing short- or long-term environmental variation can favour the evolution of specialization because the rising-tide strategy is likely to experience its optimal environmental conditions more frequently, even when the variance in fitness or variation in the population size of the rising-tide strategy is higher than that of the bet-hedging strategy (figure 3h–l). Therefore, we suggest that the relative effects of short-term environmental variation, long-term environmental variation and the mean environmental condition are non-uniform and may change according to the relative magnitude of each factor.

To more directly determine how our theoretical framework performs relative to previous approaches modelling bet-hedging, we compared our continuous-time population dynamics model with one that utilizes discrete-time population dynamics (*sensu* [38]) in order to approximate the commonly used but less realistic non-overlapping generation models (e.g. [1,9,15,22]) (figure 1c–f; see equations (2.5) and (2.6) for more details). In most of these models, the temporal scale of environmental fluctuation is often classified as either (1) coarse grain, which describes among-generation variation in environmental conditions, or (2) fine grain, which describes within-generation variation in environmental conditions [10,22]. In our comparison, we find that whether population growth is continuous or discrete is crucial for the evolution of the bet-hedging versus the rising-tide strategy (figure 5; see electronic supplementary material, table S1, for parameter values). In this discrete-time population dynamics model, when long-term environmental variation is high—which is similar to coarse grain variation in discrete-population dynamics models—the bet-hedging strategy dominates the rising-tide strategy (figure 5g–i). In other words, bet-hedging is likely to be selected for under discrete-population dynamics, which is similar to our previous finding that the non-overlapping generation setting favours a bet-hedging strategy [9,10]. By contrast, polymorphic strategies are more likely to be selected for in the overlapping generation model [31,39]. Nevertheless, a polymorphism is only favoured when both

long- and short-term environmental variation are relatively low and the mean environment deviates from the optimum (figure 5l).

4. Discussion

Here, we expand the biological relevance of bet-hedging, which we define as a strategy with lower variance and mean per capita growth rate along an environmental gradient, by explicitly considering overlapping generations and flexible population sizes. Previously, bet-hedging has been based on the concept of geometric mean fitness for organisms with non-overlapping generations [9,10,15,25] and, consequently, the original definition of lower variance and mean fitness among generations cannot be applied to many prokaryotes and most eukaryotes because they exhibit overlapping generations. Since there is no clear boundary for any generation under an overlapping generation setting in most existing theoretical treatments, we overcame this problem by establishing a continuum of biological adaptations to environmental fluctuation that includes bet-hedging (low mean and low variance of fitness) and the rising-tide (high mean and high variance of fitness). We use these alternative strategies to explore how the environmental mean and variance over different temporal scales influence biological adaptation to fluctuating environments.

Importantly, we found that the influences of different temporal scales of environmental variation on biological adaptation are strongly modulated by the mean environmental conditions relative to the performance curve optima. However, combinations of environmental mean and variance can result in rich and unexpected patterns of adaptation. For example, small, but not large, long-term environmental variation can favour the evolution of bet-hedging over rising-tide when the mean environmental condition deviates from the optimal environment of the two strategies. We also show that whether population size changes continuously or discretely, such as in species that are continuous versus seasonal breeders [40,41], can also impact biological adaptation because the rising-tide strategy is selected for under a broader range of environmental conditions than the bet-hedging strategy under continuous dynamics, whereas bet-hedging dominates under discrete dynamics. Thus, our model results are consistent with previous analytic models, which find that natural selection maximizes a compromise between a high growth rate and a small environmental variance in population growth rate in the continuous-time setting, provided that fluctuations in population size around carrying capacity are relatively small [16,30,32]. Here, we further develop a general framework for understanding the impacts of different temporal scales of environmental variation on organisms, one that can easily be applied to real-world climatic data for species living in fluctuating environments (see electronic supplementary material, figure S2, for an empirical example).

By extending the concept of bet-hedging to consider overlapping generations and variable population sizes, our model relaxes the previous restrictive assumptions of bet-hedging theory. Crucially, the distinction between within- and among-generation bet-hedging that results from the non-overlapping generation assumption of the geometric mean of fitness is clearly not applicable to many organisms, especially for relatively long-lived species.

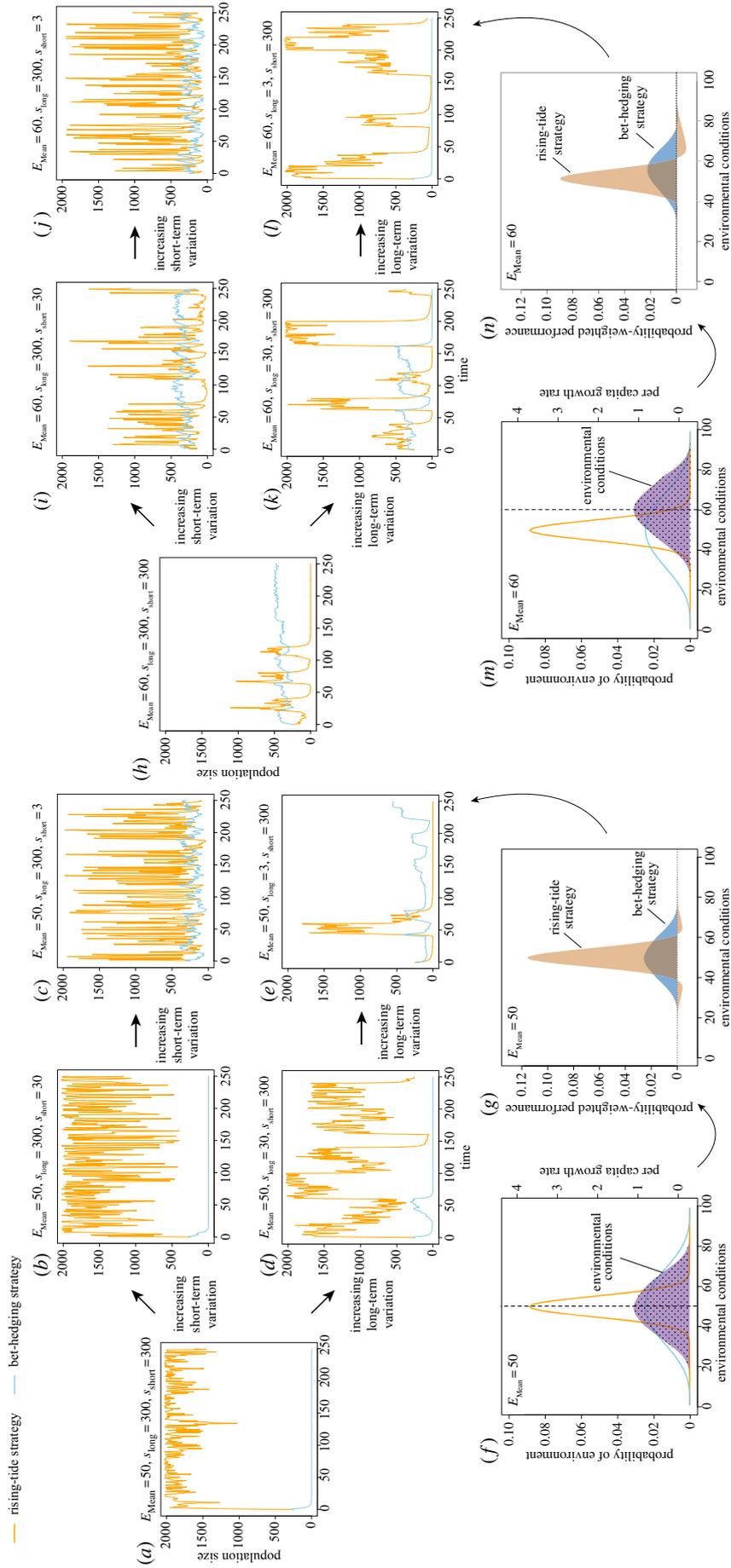


Figure 3. A demonstration of the probability of environmental conditions and the effects of different variations in population dynamics. (a–e) Population dynamics of the bet-hedging and rising-tide strategies with mean environmental conditions of 50. (f) The probability distribution of environmental conditions (purple and dotted area) and its relation to the performance curves of each strategy. (g) The probability-weighted performance (i.e. the performance curve multiplied by environmental probability) shows the realized performance among all environmental conditions. (h–l) The population dynamics of the two strategies with mean environmental conditions of 60. (m,n) Same properties as (f,g), respectively, but with mean environmental conditions of 60. E_{Mean} represents mean environmental conditions, s_{long} and s_{short} are shape coefficients for long-variation and short-term environmental variation, respectively. (Online version in colour.)

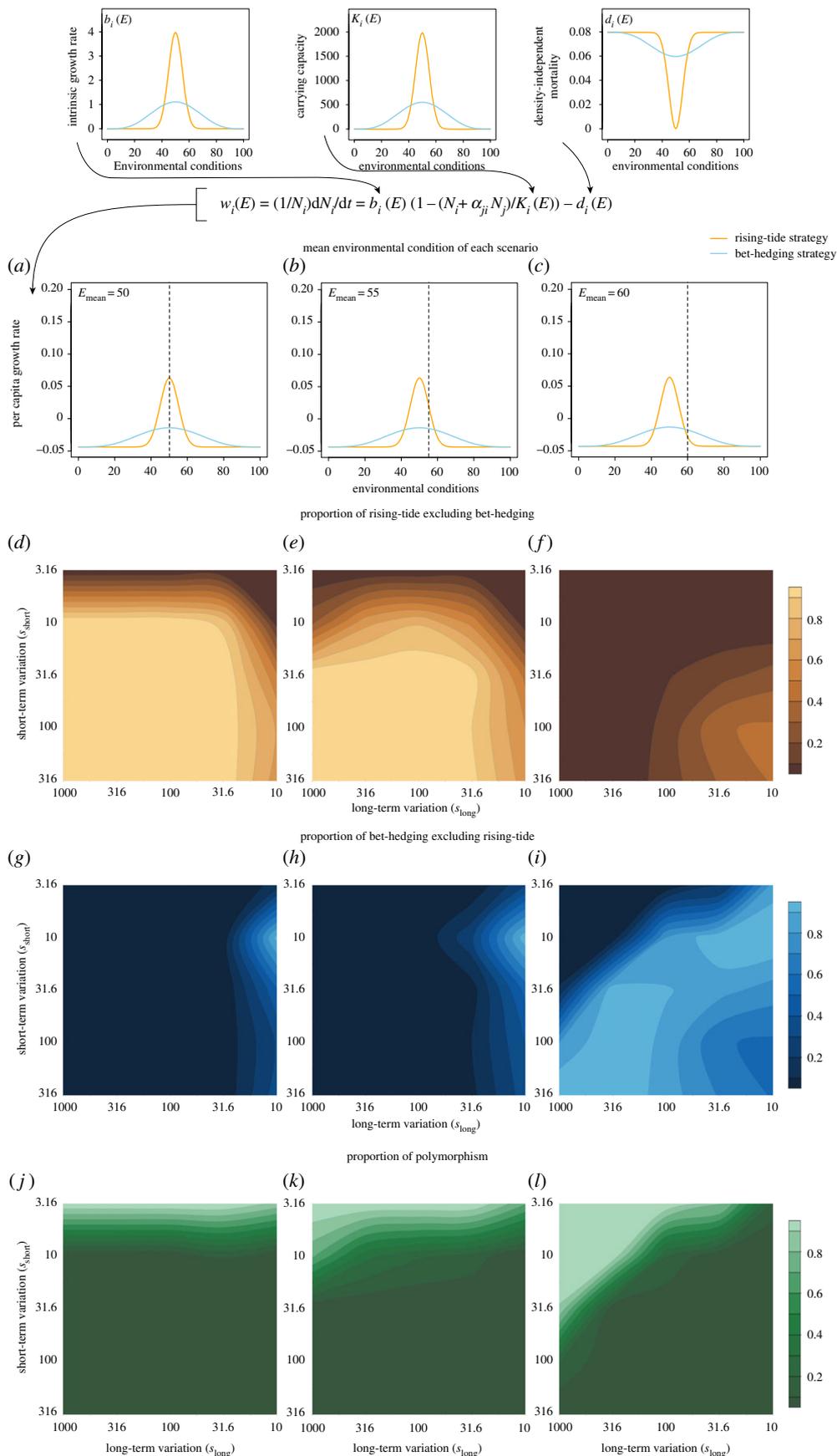


Figure 4. The proportion of simulations where the rising-tide strategy reaches fixation, the bet-hedging strategy reaches fixation or a polymorphism exists under continuous-time population dynamics. (a–c) We consider three scenarios where the mean environmental conditions (i.e. E_{mean}) move from the optimum (a) to harsher environmental conditions (b,c) and explore the outcome of the selection dynamics under each scenario. (d–f) The proportion of selection dynamic models where the rising-tide strategy excludes the bet-hedging strategy. (g–i) The proportion of selection dynamic models where the bet-hedging strategy excludes the rising-tide strategy. (j–l) The proportion of polymorphisms where both strategies coexist until the termination of simulations. Note that larger shape coefficients of beta functions (i.e. s_{short} and s_{long}) represent narrower distributions and smaller variability. Panels in the same column (e.g. (d), (g), (j)) represent the same dataset. In addition, each proportion value is calculated from 1000 repeated simulations where one simulation lasts 20 000 time units (including 20 000 short-term and 1000 long-term variations), unless any strategy dies out before termination. (Online version in colour.)

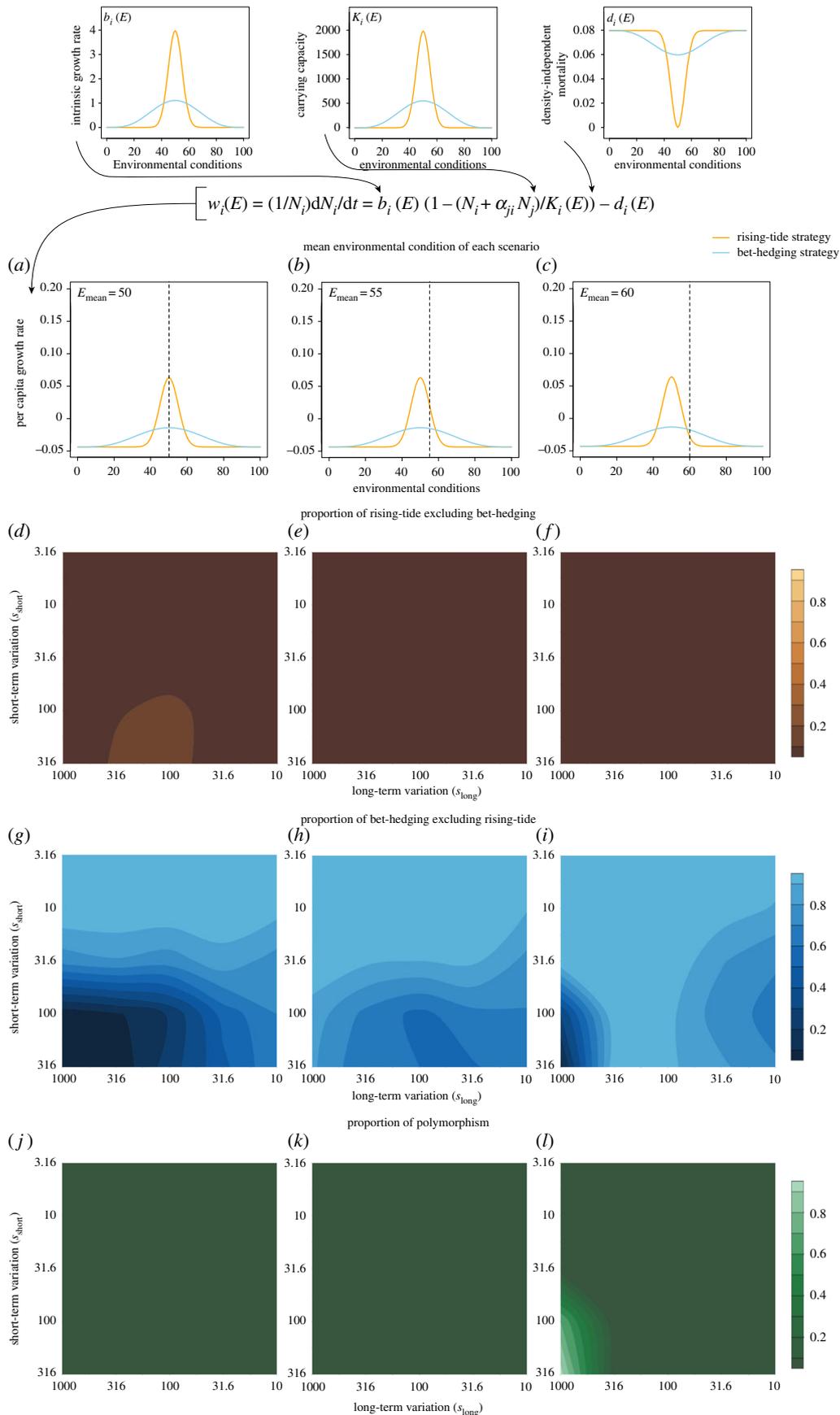


Figure 5. The proportion of simulations where the rising-tide strategy reaches fixation, the bet-hedging strategy reaches fixation, and a polymorphism exists under discrete-time population dynamics. (a–l) Each panel is analogous to that in figure 4, but simulated under discrete rather than continuous-time population dynamics. Note that although double extinction (i.e. two strategies simultaneously die) is not shown, some areas exhibit a substantial proportion of this result (e.g. lower left corner of (g), lower right corner of (h) and (i)). See figure 4 and methods for more detail. (Online version in colour.)

Although within-generation bet-hedging has generally been assumed to be rare in nature [42–44], we believe that the concept can still be used to explain many forms of adaptation to

fluctuating environments. Our model shows that lowering the variation in fitness at the expense of a lower mean fitness in fluctuating environments within the lifetime of an

organism—but not within a generation of a population, which represents a non-overlapping generation setting—can still be favoured by natural selection and constitutes a form of bet-hedging. This is because the strength of natural selection also varies according to the environment through changes in population size [45]. As population size increases in high-quality environments (e.g. good years), the strength of selection will be weaker, similar to cases of genetic surfing (i.e. genotypes can increase their size in the population quickly during population expansion [46,47]), ultimately selecting for the rising-tide strategy. By contrast, when population size decreases in low-quality environments (e.g. bad years), the strength of selection will be stronger, similar to a population going through a bottleneck [48,49], ultimately selecting for the bet-hedging strategy. Thus, a strategy that can have higher relative fitness in bad years can increase its frequency in the population substantially. All else being equal, producing an offspring when a population is small (e.g. in a bad year) contributes more to the long-term fitness of a genotype than doing so when a population is large because it increases the frequency of the focal genotype more. To illustrate this, consider that producing one individual in a population of 10 000 contributes a 0.01% increase in the focal genotype, compared with a 1% increase of the genotype if the population size is only 100 [21]. Therefore, simply summing the number of offspring produced is not a proper fitness measure of what natural selection maximizes in cases of fluctuating population size with overlapping generational life histories [21,50]. Thus, the contrasting selection forces between good and bad years will jointly determine where the biological adaptation occurs along the continuum of adaptations to environmental fluctuation.

Similarly, life-history theory predicts that higher long-term environmental variation selects for survival generalists [51] and for reproduction generalists [18], but that higher short-term environmental variation selects for survival generalists [51] and reproduction specialists [18]. However, these predictions are based on (1) the geometric mean of fitness with a non-overlapping generation assumption and (2) fixed or infinite population sizes, which assumes that within-generation reproduction is additive and among generation reproduction is multiplicative. By contrast, for organisms with overlapping generations and variable population sizes, birth and death events can occur at the same time intervals, which also means that fitness can no longer

be partitioned into within- and among- generation components and thus the additive and multiplicative fitness calculation are invalid. Instead, population dynamics need to be considered when calculating individual reproductive values, something that theoreticians have only just begun to address [16,52–54]. Nevertheless, as we have shown in our model (and in the electronic supplementary material), the effect of temporal scales of environmental variation and their interactions with the mean condition can result in diverse reproductive and survival strategies, most of which are still largely unexplored. Furthermore, previous studies have shown that biological adaptations to fluctuating environments will also depend on how mean environmental conditions have changed in the past (e.g. speed, predictability, frequency) [55,56]. Although we do not consider these factors here, we believe that doing so will be fruitful for future studies.

In conclusion, we suggest that researchers should move beyond viewing environmental variation as discrete classes of coarse (among-generation) and fine grain (within-generation), and instead begin investigating the existence of a potentially rich suite of adaptations to diverse environmental scenarios—those that vary in intensity, frequency, and duration—in an ever-changing world. Ultimately, our study not only helps bridge the apparent gap between theoretical and empirical studies of biological adaptation in a volatile world, but it also develops a synthetic theoretical framework that links seemingly distinct fields, such as life-history evolution [18,49], macrophysiology [57] and species distribution modelling [17,58].

Data accessibility. All simulated data was generated using the C language. The code used for this study is available at https://github.com/mingpapilio/Codes_RisingTide.

Authors' contributions. S.-F.S. conceived the idea. M.L., W.-C.L. and S.-F.S. constructed the models. M.L., D.R.R. and S.-F.S. designed the study, analysed the data and wrote the paper.

Competing interests. We declare we have no competing interests.

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