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# Evolutionary bet-hedging reconsidered: What is the mean–variance trade-off of fitness?

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**Abstract**

In traditional theories, bet-hedging in evolutionary biology is defined as a trade-off between the within-generation arithmetic mean fitness (AMF) of a genotype and between-generation variance (BGV) in AMF across generations. The rationale of this definition is that a bet-hedger genotype suppresses the BGV to increase between-generation geometric mean fitness (GMF; an index of long-term sustainability), which in turn entails costs in terms of AMF. However, too strict interpretation of this definition causes confusion among empirical researchers. For example, in empirical studies comparing a putative bet-hedger (e.g., producing a generalist phenotype or mixture of various phenotypes) and non-bet-hedger control (e.g., producing only a specialist phenotype), reviewers sometimes request that a necessary condition of bet-hedging is that the bet-hedger candidate shows a smaller arithmetic mean of AMFs obtained from multiple generations and larger GMF than the control. However, the cost of bet-hedging is incurred at the potential genotypic level and thus the decrease of AMF mean is not necessarily observed at the phenotypic level (especially if bet-hedger individuals have good conditions). Moreover, contrary to previous arguments, the "fine-grained" environments would promote bet-hedging because even monomorphic specialist genotypes increase GMF if their population size is sufficiently large. Computer simulations support these views. I try to shift the definition of bet-hedging from the trade-off-based one to the GMF-based one: bet-hedging is any strategy to increase the between-generational GMF to avoid extinction of its controlling genotype against unpredictable environmental fluctuation. Under this new light, bet-hedging will be a universal law of biology.

**KEYWORDS**

environmental grain, evolution, geometric mean fitness, long-term sustainability, trade-off

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# 1 | INTRODUCTION

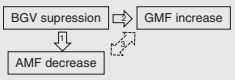
## 1.1 | Adaptations under uncertainty

Organisms live in unpredictably changing environments (Levins, 1968; Stearns, 1992). Annual plants need to produce seeds without knowing the growing environment (e.g., temperature and rainfall) in the next spring (Cohen, 1966) and birds cannot determine beak size after looking at their prey (Iwasa, 1990). Butterflies have to lay eggs on a food plant without knowing whether large herbivores such as cows will graze on the entire plant (Hopper, 1999; Root & Kareiva, 1984). Female animals have to mate with a male whose (genetic or environmental) qualities, which sometimes lead to reproductive failure (no surviving offspring), are unknown (Yasui, 2001; Yasui & Garcia-Gonzalez, 2016). If all mothers of the same genotype (strategy) fail to reproduce for these reasons, the genotype goes extinct. In such situations, bet-hedging strategies to perform risk avoidance or risk spreading achieve long-term (multigenerational) sustainability (Philippi & Seger, 1989; Slatkin, 1974; Starrfelt & Kokko, 2012).

## 1.2 | How to calculate fitness

The index used to evaluate the performance of a bet-hedging strategy is the geometric mean fitness (GMF: Table 1 shows all abbreviations, definitions and equations used in this study) of its controlling genotype (Gillespie, 1974, 1977; Yasui & Yamamoto, 2021; Yoshimura & Clark, 1991; Yoshimura & Jansen, 1996). More than one individual of the same genotype usually exists, and fitness varies among the individuals so that some average value should be calculated to represent the genotypic fitness (Figure 1). Here, the number of surviving offspring until maturation is adopted as fitness. When a mother (e.g., butterfly) lays five, three, and six eggs on three different plants and 4, 0, and 3 offspring from these eggs successfully reach adulthood, respectively, the individual fitness (IF) of this mother is the sum of scores ($4 + 0 + 3 = 7$). If there are three mothers of the same genotype with IF values of 7, 10 and 0 in the same generation, the within-generation mean fitness of the genotype is the arithmetic mean fitness (AMF) over all mothers: $\mathrm{AMF} = \frac{7+10+0}{3} = 5.67$. If more than one population (e.g., 5, 8, 14, and 3 in another population) exists, the IF of different populations could be pooled $\left(\mathrm{AMF} = \frac{7+10+0+5+8+14+3}{7} = 6.71\right)$ or evaluated while maintaining population structure $\left(\mathrm{AMF} = \frac{\frac{7+10+0}{3}+\frac{5+8+14+3}{4}}{2} = 6.585\right.$, Figure 1), depending on the study purpose. When three successive (discrete for simplicity) generations exist (e.g., each with an AMF = 6.585, 11.31, or 7.13), the between-generation mean fitness should be the GMF across generations: $\mathrm{GMF} = \sqrt[3]{6.585 \times 11.31 \times 7.13} = 8.097$. Note that, because the reproductive events of different individuals (7, 10, and 0 in Figure 1 example) or different clutches (distributed in different places or environments) produced by the same mother (4, 0, and 3 in the Figure 1) are mutually (at least conceptually) independent events, their average should be the arithmetic mean because of their additive nature. On the other hand, the number of individuals in the present generation is the result of reproduction in the previous generation(s). This is the reason why fitness across generations has a multiplicative nature. Because the present is subordinate to the past, the average across generations should be a geometric mean (e.g., a fitness score of 0 in the previous generation cannot lead to fitness scores other than 0 in the present generation; in other words, using the AMF across generations is nonsensical). The characteristic nature of the geometric mean is that it strongly depends on small values in the dataset (Yasui & Garcia-Gonzalez, 2016). In particular, if the dataset contains 0, the geometric mean necessarily becomes 0. This implies that if only one generation resulting in AMF = 0 is included, the genotype or lineage goes extinct even if the other generations are very successful $\left(\text{e.g., GMF} = \sqrt[3]{6.585 \times 100 \times 0} = 0\right)$. Thus, organisms must maintain a GMF > 0 to avoid extinction. The strategies achieving higher GMF by suppressing the intergenerational fluctuation of AMF are generically called bet-hedging strategies (Yasui, 1998; Yasui, 2001; Yasui & Garcia-Gonzalez, 2016). A conservative bet-hedger genotype, producing a single phenotype with risk-avoidance nature (e.g., production of diapausing eggs earlier than the environmental deterioration), maintains relatively constant moderate values of fitness over generations $\left(\text{e.g., GMF} = \sqrt[4]{5 \times 5 \times 5 \times 5} = 5\right)$. On the other hand, a diversified bet-hedger genotype, producing multiple phenotypes each adapted to different environments (e.g., production of diapausing and nondiapausing eggs), (arithmetically) averages good and bad scores within each mother $\left(\text{e.g., GMF} = \sqrt[4]{\frac{8+2}{2} \times \frac{8+2}{2} \times \frac{8+2}{2} \times \frac{8+2}{2}} = 5\right)$ and both types of bet-hedgers achieve a higher GMF than a non-bet-hedger or non-bet-hedging (NBH) $\left(\text{e.g., GMF} = \sqrt[4]{8 \times 2 \times 8 \times 2} = 4\right)$. Bet-hedging adaptation is widespread among animals and plants, for example, the partial germination of dormant seeds (Cohen, 1966),

**TABLE 1** List of abbreviations

| Abbreviations | Term | Definition | Formulation |
|---|---|---|---|
| IF | Individual fitness | Lifetime total of fitness score $w$ (typically, the number of matured offspring) of individual $i$, reproducing $f$ times | $x_i = \sum_{e=1}^{f} w_e$ |
| AMF | Arithmetic mean fitness | Average of IF among $n$ individuals of a focal genotype within a generation | $\frac{1}{n}\sum_{i=1}^{n} x_i$ |
| WGV | Within-generation variance of fitness | Variance in IF among $n$ individuals of a focal genotype within a generation | $\frac{1}{n}\sum_{i=1}^{n} (x_i - \mathrm{AMF})^2$ |
| AMAMF | Arithmetic mean of AMFs | Arithmetic average of AMF across $g$ generations (conceptual value) | $\frac{1}{g}\sum_{j=1}^{g} \mathrm{AMF}_j$ |
| GMF | Geometric mean fitness | Geometric average of AMF across $g$ generations | $\sqrt[g]{\prod_{j=1}^{g} \mathrm{AMF}_j} = \exp\left[\frac{1}{g}\sum_{j=1}^{g} \ln \mathrm{AMF}_j\right]$ |
| BGV | Between-generation variance of fitness | Variance in AMF over $g$ generations | $\frac{1}{g}\sum_{j=1}^{g} \left(AMF_j - AMAMF\right)^2$ |
| NBH | Non-bet-hedging or non-bet-hedger | Strategies to increase AMF while increasing BGV (= extinction risk) | Small GMF $= \sqrt[g]{\prod_{j=1}^{g} \mathrm{AMF}v_j}$<br>AMF$v$: highly variable AMF |
| BH | Bet-hedging or bet-hedger | Strategies achieving higher between-generation GMF by suppressing the intergenerational fluctuation of within-generation AMF | Based on hypothetical (1) positive correlation between AMF and BGV, (2) negative correlation between BGV and GMF, and (3) potential negative correlation between AMF and GMF   |
| CBH | Conservative bet-hedging or conservative bet-hedger | BH is achieved by the individual's suppression of BGV, maintaining suboptimal but constant AMF | large GMF $= \sqrt[g]{\prod_{j=1}^{g} \mathrm{AMF}c_j}$<br>AMF$c$: suboptimal but constant AMF |
| DBH | Diversified bet-hedging or diversified bet-hedger | A single mother lays a polyphenic clutch, in which individuals of fit phenotype to the environment survive and maintain moderate IF of the mother (offspring of unfit phenotype die). Averaging of relatively constant IFs between $n$ mothers results in moderate AMF and small BGV (= large GMF) | Large GMF $= \sqrt[g]{\prod_{j=1}^{g} \left(\frac{1}{n_j}\sum_{i=1}^{n_j} \mathrm{IF}c_{j,i}\right)}$<br>IF$c$: suboptimal but constant IF |
| MLDBH | Multi-lineage diversified bet-hedging | A single mother produces offspring of a single phenotype but different mothers produce different phenotypes. Arithmetic averaging of highly-variable IFs between $n$ mothers results in moderate AMF and small BGV (= large GMF) | Large GMF $= \sqrt[g]{\prod_{j=1}^{g} \left(\frac{1}{n_j}\sum_{i=1}^{n_j} \mathrm{IF}v_{j,i}\right)}$<br>IF$v$: highly variable IF |
| WGDBH | Within-generation diversified bet-hedging | Individuals live longer over multiple reproductive seasons or move across multiple habitats and reproduce $f$ times (i.e., overlapping generations). The summation of $f$ fitness scores offsets the fluctuation of reproductive success among seasons, resulting in non-zero IF of individual $i$, moderate AMF among $n$ individuals and small BGV and large GMF across $g$ generations. Consequently, BH is achieved | GMF $= \sqrt[g]{\prod_{j=1}^{g} \left(\frac{1}{n}\sum_{i=1}^{n}\sum_{e=1}^{f} w_{j,i,e}\right)}$<br>$w_{j,i,e}$: fitness score in reproductive event $e$ of individual $i$ in generation $j$ |

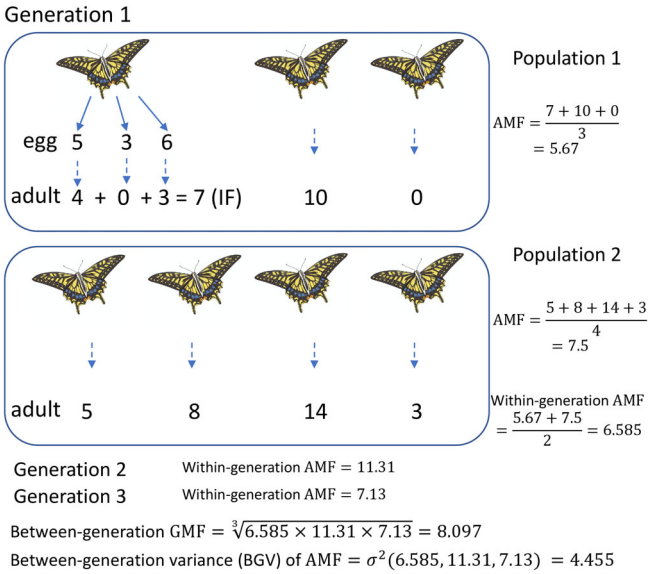



**FIGURE 1** Various concepts of the mean and variance of fitness. The total number of matured offspring in multiple clutches laid by a female butterfly is individual fitness (IF). Arithmetic mean fitness (AMF) is calculated among all females of the same genotype across populations within a generation. Geometric mean fitness (GMF) is calculated across AMFs of multiple generations. Between-generation variance (BGV) of AMF is necessarily (mathematically) negatively correlated with GMF, but the positive correlation between BGV and AMF is simply an assumption. See the text [Color figure can be viewed at wileyonlinelibrary.com]

submaximal clutch size (Charnov & Krebs, 2008), egg dispersal over multiple patches (Root & Kareiva, 1984), iteroparity (Philippi & Seger, 1989; Stearns, 1992) and female multiple mating (Yasui, 1998; Yasui, 2001; Yasui & Garcia-Gonzalez, 2016; but see Holman, 2016), and, in fact, one of the fundamental laws of biological evolution.

## 1.3 | The mean–variance trade-off is sometimes unobservable

Philippi and Seger (1989) defined bet-hedging as "a trade-off between the mean (A) and variance of fitness, such that phenotypes with reduced mean (B) fitness may be at a selective advantage under certain conditions" ((A) and (B) are added by the present author). However, this definition is quite ambiguous. Do mean (A) and mean (B) indicate the same parameter, and which mean (AMF or GMF) do they imply? At which level (within-generational or between-generational) is the variance considered? As mentioned above, bet-hedging is a concept regarding long-term sustainability, and thus, the "variance" should be between-generational. Because the GMF is the objective function of bet-hedging adaptation, the reduced mean (B) fitness should not be the GMF but AMF (represented by its intergenerational arithmetic mean, AMAMF; see Table 1). The mean (A) should be the intergenerational geometric mean (GMF). Therefore, the definition is interpreted as the trade-off between GMF and between-generation variance (BGV) of AMF. This definition would be that bet-hedging traits (e.g., seed dormancy; Cohen, 1966) suppressing intergenerational fitness fluctuations (BGV) and increasing GMF is costly in terms of AMF (momentary rate of increase). Here, another trade-off (negative correlation) is also expected between GMF and AMAMF as a result of a positive correlation between AMAMF and BGV. This GMF-AMAMF trade-off has been thought as a key feature of bet-hedging. However, too strict an interpretation of this trade-off has caused problems. Experimental studies are sometimes requested (by reviewers) that a putative bet-hedger shows a smaller AMAMF and larger GMF than a non-bet-hedger control (Childs et al., 2010; Starrfelt & Kokko, 2012) such as Case 1 in Table 2. However, the suppression of BGV does not necessarily reduce the AMF (Case 2 in Table 2). The parameter ranges enabling the "lose in terms of AMF but win in terms of GMF" rule seem very narrow.

Reviewing the history of BH definitions (Table 3), Slatkin (1974) expected a negative correlation (trade-off) between GMF and BGV only at the comparison between strategies with the same AMAMF. However, in empirical studies, the adjusting AMAMF equal is almost impractical, so that his definition has only conceptual meaning. The later authors (Philippi & Seger, 1989; Seger & Brockmann, 1987) did not mention the condition of equal AMF. Starrfelt and Kokko (2012) and Haaland et al. (2019), in turn, implicitly admitted that the AMF reduction is not necessary.

Such a misuse of the trade-off-based definition is caused by confusing potential costs at the genotypic level with realized decrease of fitness at the phenotypic level. For example, an individual with a bet-hedger genotype with environmentally good conditions would be superior to that with a non-bet-hedger genotype with bad conditions even if the former incurs an unavoidable cost. In an empirical test (Yasui & Yamamoto, 2021) of the bet-hedging polyandry hypothesis (Yasui & Garcia-Gonzalez, 2016) using the field cricket *Gryllus bimaculatus*, females in the polyandrous treatment (assumed as diversified bet-hedgers, DBHs) showed a higher AMF in some generations than females in the monandrous treatment (as NBHs), which resulted in a higher GMF across generations. Therefore, a negative correlation between AMF and GMF may occur at the genotypic level but would not necessarily be observed at the realized phenotypic level. The overly strict

**TABLE 2** "Lose in terms of arithmetic mean fitness (AMF) but win in terms of geometric mean fitness (GMF)" is difficult

| Case 1 | Genotype A | | Genotype B | Case 2 | Genotype A | | Genotype B |
|---|---|---|---|---|---|---|---|
| AMF in Generation 1 | 10 | > | 9 | AMF in Generation 1 | 10 | > | 9 |
| AMF in Generation 2 | 15 | > | 9 | AMF in Generation 2 | 15 | > | 9 |
| AMF in Generation 3 | 1 | < | 7 | AMF in Generation 3 | 1 | < | 9 |
| AMAMF | 8.6667 | > | 8.3333 | AMAMF | 8.6667 | < | 9 |
| BGV | 33.5556 | > | 0.8889 | BGV | 33.5556 | > | 0 |
| GMF | 5.3133 | < | 8.2768 | GMF | 5.3133 | < | 9 |

*Note*: In Case 1, the BGV reduction in Genotype B results in the negative correlation between the AMAMF and GMF. However, the slight increase of AMF in Generation 3 (Case 2) turns the correlation positive.
Abbreviations: AMAMF, arithmetic mean of arithmetic mean fitness; AMF, arithmetic mean fitness; BGV, between-generation variance; GMF, geometric mean fitness.

**TABLE 3** The definition history of bet-hedging

| Literature | Definition |
|---|---|
| Slatkin (1974) | An allele which produces *the same mean number* of offspring but a smaller variance will increase in frequency |
| Seger and Brockmann (1987) | Individuals actually suffering a loss of expected or average fitness in order to reduce the variance of fitness |
| Philippi and Seger (1989) | A trade-off between the mean and variance of fitness, such that phenotypes with reduced mean fitness may be at a selective advantage under certain conditions |
| Starrfelt and Kokko (2012) | A strategy or allele that increases the probability of its fixation by lowering the variance of fitness *even though* mean (arithmetic) fitness declines |
| Haaland et al. (2019) | Bet-hedging has been defined as a strategy increasing its probability of fixation in the population through decreasing the variation in fitness across generations despite also decreasing mean fitness. … the success of a lineage over time is best estimated by geometric mean fitness across generations rather than the arithmetic mean. … a genotype experiencing *less variation in fitness across generations* can spread despite having *a lower expected fitness in any one generation* |
| Present study | Strategies to increase the between-generational GMF to avoid extinction of its controlling genotype against unpredictable environmental fluctuation. It is potentially costly in terms of AMF but this cost is sometimes unobservable |

interpretation of the trade-off-based definition narrows the scope of application of bet-hedging. For example, in an evaluation of the strength of the evidence about bet-hedging in 103 studies, Simons (2011) found only 12 studies that provided strong evidence based on the GMF evaluation (Hopper, 2018). Removing this restriction, bet hedging can be more common than previously thought. In this paper, I try to shift the definition of bet-hedging from the trade-off based one to the GMF based one (Table 3).

## 1.4 | What is the environmental grain and why is it important?

One important but frequently misunderstood concept is "environmental grain" (Levins, 1968; Starrfelt & Kokko, 2012; Yasui & Garcia-Gonzalez, 2016). Here, I define it as the relative size of a single environmental type to the spaciotemporal distribution of the focal genotype (strategy) (see Figure 2). The size of a coarse-grained environment (Figure 2a) is larger than the moving range of a population of each genotype, meaning that all individuals in the same generation experience the same condition such as wet or dry summer. The environments unpredictably change over generations. In such situations, the specialist genotypes (Ws and Ds in Figure 2a) exhibit higher fitness fluctuation between generations because all Ws individuals are favored in a wet-conditioned generation but unfavored in a dry-conditioned generation (i.e., they are NBH because of large BGV; Table 4). Consequently, it causes small GMF (higher extinction risk). A conservative bet-hedging (CBH) genotype produces a single generalist phenotype to cope with both environmental types and exhibits moderate but relatively constant AMF throughout generations, resulting in small BGV and large GMF (Table 4). In a diversified bet-hedging (DBH) genotype, a single parent produces offspring

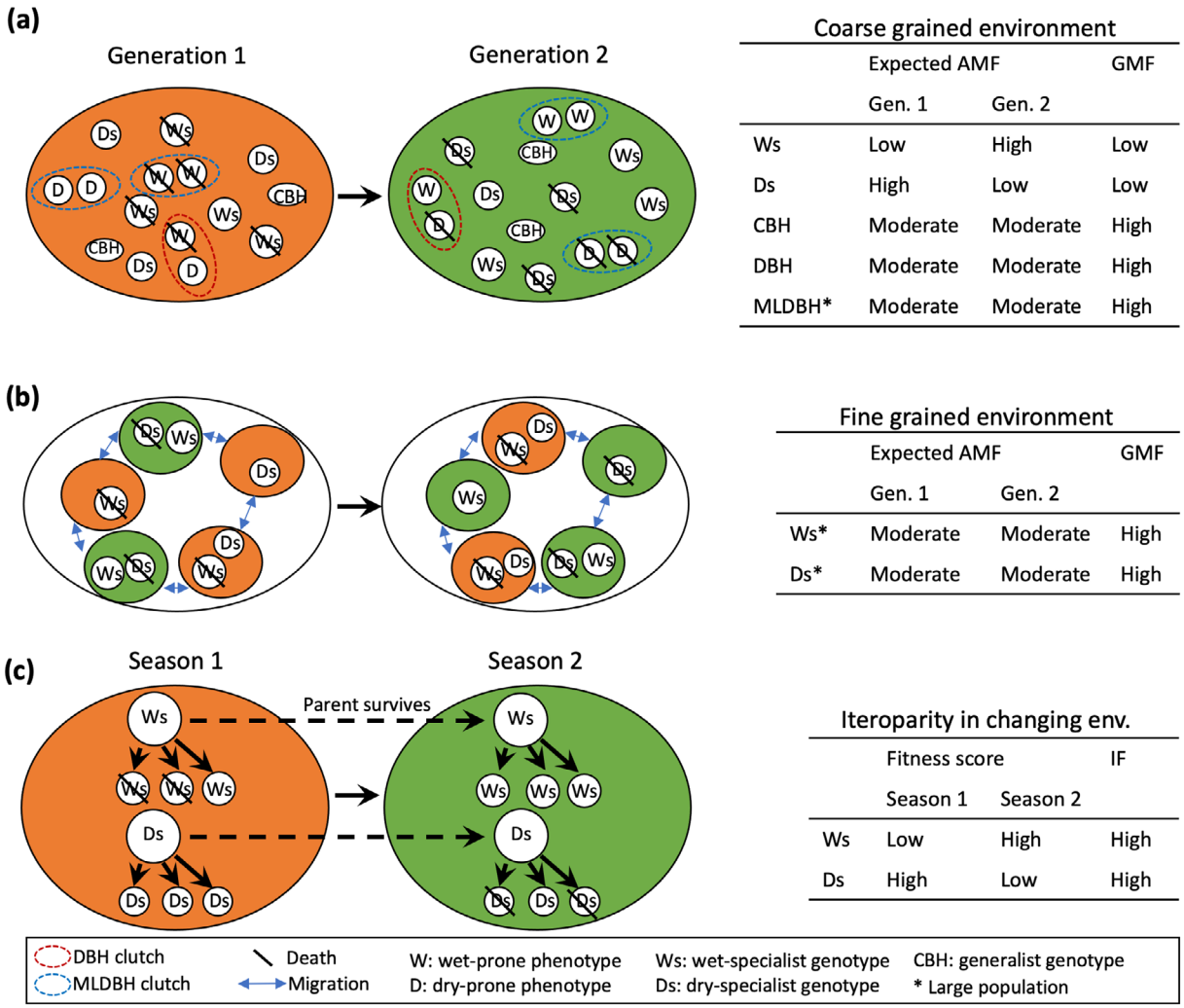



**FIGURE 2** Environmental grain concepts. (a) In a coarse-grained environment, all individuals of the same genotype are equally affected by environmental conditions (the fitness correlation between individuals is high). Specialist genotypes (wet specialist, Ws or dry specialist, Ds) produce only one phenotype in offspring. Conservative bet-hedger (CBH) produces a single generalist phenotype. A diversified bet-hedger (DBH) parent produces multiple phenotypes in an offspring clutch (wet-prone phenotype, W and dry-prone phenotype, (d). A multilineage diversified bet-hedger (MLDBH) parent produces only one phenotype in offspring but different parents produce different phenotypes. The between-generation fluctuation in arithmetic mean fitness (AMF) is large in Ws and Ds but small in CBH, DBH, and MLDBH (if population size is sufficiently large). (b) In a fine-grained environment, the environment varies within dispersal range of a genotype. The fitness correlation between individuals is low. If population size is sufficiently large, even the specialist genotypes achieve large geometric mean fitness (GMF). (c) A single iteroparous parent experiences different environment over multiple reproductive seasons. Individual fitness (IF) is a summation of fitness scores over seasons, absorbing the fitness fluctuation. See the text. Gen., generation; env., environment [Color figure can be viewed at wileyonlinelibrary.com]

of multiple specialist phenotypes (W and D) according to an adaptive proportion; typically, the occurring probability of each environmental type (Iwasa, 1990). For example, if wet summer and dry summer come at $p$: 1 – $p$ proportions, a mother produces W and D at $p$: 1 – $p$ in a clutch. At least some ($p$ or 1 – $p$) offspring in a clutch survive in either condition and thus, IF of the parent, AMF of the genotype become moderate and constant values, resulting in small BGV and large GMF (Table 4). However, when a single parent produces only one type of offspring but different parents produce different types, such that $p$ mothers produce W and 1 – $p$ mothers produce D, arithmetic averaging across multiple parents results in intermediate AMF, small BGV, and large GMF (Table 4). I name this strategy as "multi-lineage diversified bet-hedging" (MLDBH). Note that the compensation of fitness variance occurs at the individual level in CBH (all parents play it safe) and DBH (all parents do not put all eggs in a single basket) but at the

TABLE 4 The relationships between parameters in each concept

| | IF | WGV | AMF | BGV | GMF |
|---|---|---|---|---|---|
| NBH (coarse grained or small population) | High or low | Small[a] | Large or small | Large | Small |
| NBH (fine grained or large population) | High or low | Large[b] | Moderate | Small | Large |
| CBH | Moderate | Small[c] | Moderate | Small | Large |
| DBH | Moderate | Small[d] | Moderate | Small | Large |
| MLDBH (large population) | High or low | Large[b] | Moderate | Small | Large |

[a]All IFs are high or low.
[b]High IFs and low IFs co-occur.
[c]All IFs are intermediate value.
[d]High fitness scores and low fitness scores are offset within each parent.
Abbreviations: AMF, arithmetic mean fitness; BGV, between-generation variance of fitness; CBH, conservative bet-hedging; DBH, diversified bet-hedging; GMF, geometric mean fitness; IF, individual fitness; MLDBH, multi-lineage DBH; NBH, non-bet-hedging; WGV, within-generation variance of fitness.

genotypic level in MLDBH (some parents are successful but others are not) (Table 4). To achieve the same GMF as DBH, MLDBH needs the large population size containing all phenotypes at W: D = $p$: 1 – $p$.

In fine-grained environments (Figure 2b), the moving range of individuals of the same genotype is larger than the size of a single environmental type. Different individuals experience different environments. Imagine the case that butterfly eggs on some host plants (proportion $p$) are eliminated by grazing of large herbivore animals, but eggs laid by the same mother on other plants (1 – $p$) are intact. This egg-dispersing strategy is a sort of "within-generation bet-hedging" (Hopper et al., 2003; Starrfelt & Kokko, 2012). However, if population size is sufficiently large, even NBH (egg-concentrating on a single host) strategy can absorb fitness fluctuation at the genotypic level (Table 4) because the failure of $p$ mothers losing all eggs is compensated with the success of 1 – $p$ mothers suffering no predation. This is the reason why bet-hedging in fine-grained environments has not been believed to work effectively (Hopper et al., 2003).

However, rather than to say that the within-generation bet-hedging strategies are no longer effective in large populations in fine-grained environments, it is more accurate to say that the existence of many NBH individuals is now acting as bet-hedging. Note that, the logical structure of the NBH in fine-grained environment is equal to that of MLDBH regarding the fitness consequence (Table 4), namely, the fitness compensation occurs between successful and unsuccessful mothers within the same genotype. Although within-generation variance of fitness (WGV) is large in these strategies, arithmetic averaging among many mothers would result in moderate AMF, small BGV and finally large GMF (Table 4).

Likewise, iteroparity over multiple reproductive seasons (typically years; Figure 2c) creates a temporally fine-grained environment because a single long-living parent could reproduce both in favorable and unfavorable environments. In this case, the moving range (along a time axis) of individual is also larger than the duration of a single environmental type. Thus, even the specialist genotype producing only one phenotype can leave some offspring to the next generation if at least one of the reproductive seasons turns to good condition. Iteroparity or partial hatching of dormant eggs are typical "temporal bet-hedging" (Hopper, 1999).

From these considerations, I am aware that (spatially or temporally) fine-grained environments alter a specialist genotype (NBH) into some kind of bet-hedger (Table 4) if their population size is sufficiently large to cover both favorable and unfavorable environmental types.

In this study, using computer simulations, I show (1) that "it loses in terms of the arithmetic mean but wins in terms of the geometric mean" is not a necessary condition for bet-hedging in empirical studies and (2) the effects of fine-grained environments on the sustainability of specialist genotypes. Finally, I try to reconceptualize bet-hedging and discuss its ubiquity in evolutionary biology.

## 2 | COMPUTER SIMULATIONS

### 2.1 | Basic settings

Programs were written in Mathematica (Wolfram language) for Windows ver. 12.2 (Wolfram Research). The fitness scores (the number of surviving offspring) of three strategies (genotypes), that is, an NBH, a CBH, and a DBH, were compared. For simplicity, they reproduced asexually (offspring employed the same strategy as the parent). NBH and CBH mothers reproduced only once, while DBH mothers reproduced multiple times. For a single reproductive event, the fitness score was obtained by drawing a random number following a normal distribution

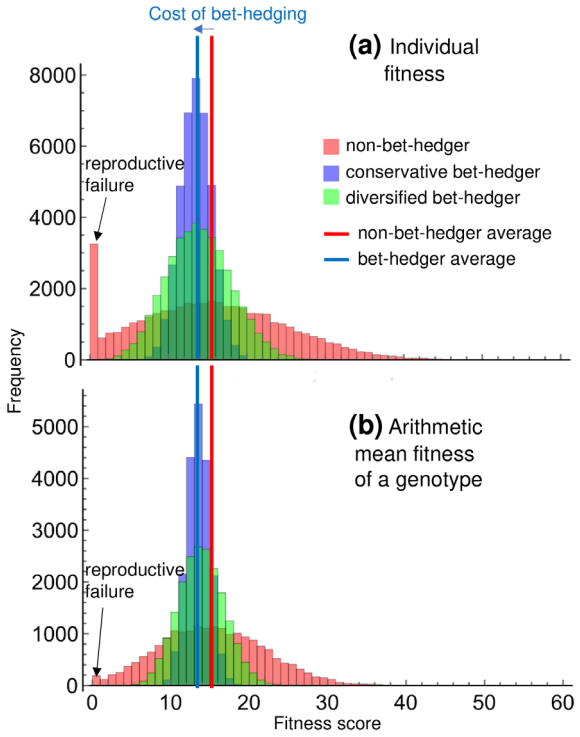



**FIGURE 3** The frequency distributions of the phenotypic (realized) fitness expected for the three strategies (genotypes). The bet-hedgers had a smaller arithmetic mean fitness ($\mu$) and a smaller standard deviation ($\sigma$) than the non-bet-hedgers. The difference in $\mu$ indicates the potential cost of bet-hedging. (a) Distribution of individual fitness (IF). A total of 40,000 fitness values (a single reproduction of 4000 mothers across 10 generations for the non-bet-hedgers (NBHs) and conservative bet-hedgers (CBHs) and an average of 5 reproductions of 4000 mothers across 10 generations for the diversified bet-hedgers (DBHs)) were pooled. Original distribution (phenotypic value) of the NBH with $\mu = 15$ and $\sigma = 10$ was altered to $\mu = 15.3285$ and $\sigma = 9.45425$ after resetting $x < 0$ to $x = 0$. The settings of the NBH were constant while those of the CBH and DBH were varied to find the evolutionary conditions of bet-hedging. In this example where bet-hedgers entail 10% cost (1.5 reduction in $\mu$), the realized values were $\mu = 13.4947$ and $\sigma = 2.00739$ for the CBH and $\mu = 13.8995$ and $\sigma = 4.13996$ for the DBH reproducing five times. Note that resetting $x < 0$ to $x = 0$ slightly increased the average in DBH (CBH did not bear negative values). (b) Distribution of within-generation arithmetic mean fitness (AMF) obtained by averaging two independently fluctuating groups of individuals (i.e., the degree of environmental grain $evg = 2$). See the text [Color figure can be viewed at wileyonlinelibrary.com]

(mean $\mu = 15$ and *SD* $\sigma = 10$ for NBHs). This can be interpreted as follows: the NBH genotype that codes for a trait value with $\mu = 15$ expresses a phenotypic distribution (Figure 3a) with environmental variance $\sigma^2 = 100$ according to developmental conditions. Drawn random numbers ($x$) less than 0 were reset to $x = 0$ (i.e., reproductive failure). The NBHs had a higher genotypic mean and wider phenotypic range of fitness than the bet-hedgers. Because a single NBH mother reproduced only once (Figure 3a), failure frequently occurred (ca. 6.5% of 40,000 reproductive events in this example). This means that the NBH strategy is the "high-risk, high-return" strategy. In CBHs, mothers also reproduced only once but suppressed their fitness variance under the same environment as NBHs (in the example of Figure 3, $\mu = 13.5$ and $\sigma = 2$, meaning a phenotypic variance $\sigma^2 = 4$ around the genotypic trait value with $\mu = 13.5$). Each DBH mother reproduced repeatedly and suppressed fitness fluctuations by averaging her own multiple reproductive events (in the example of Figure 3, $\mu = 13.9$ and $\sigma = 4.14$ after averaging 5 samples from the $\mu = 15$ and $\sigma = 10$ distribution, creating a phenotypic variance $\sigma^2 = 17.14$ around the genotypic trait value with $\mu = 13.9$). Thus, the reduction in fitness variance was achieved by the intrinsic risk-avoidance nature of the CBH strategy, while it came from the offsetting large within-mother variance under the DBH strategy (the variance is large within mothers but small between mothers). The suppression of fitness variance entails a cost and lowers the IF of bet-hedgers (Figure 3a). Thus, CBHs and DBHs display "low-risk, low-return" strategies.

## 2.2 | Environmental grain

Environmental grain is the degree of synchrony of surrounding environments among individuals. Coarse-grained environments are more synchronized than fine-grained environments (compare Figure 2a and Figure 2b). In this study, the degree of environmental grain was simulated as the number ($evg = 1$–5) of independent environmental conditions (e.g., no. patches in Figure 2) in a population. In the same patch, all individuals were synchronously affected by the same conditions. For example, if $evg = 1$, the entire population was equally affected by a coarse-grained environment (Figure 2a) and the fitness correlation between individuals of the same genotype was high (Starrfelt & Kokko, 2012). If $evg = 5$, five independent patches existed in a population. Each patch experienced different microenvironments (Figure 2b). Because IF coincided within each patch but was independent between patches, I ignored the number of individuals in each patch for simplicity and focused the number of independent patches (i.e., the degree of environmental grain $evg$). Intermediate $evg$ (2–4) simulated medium-grained or mixed environments (coarse- or fine-grained environments are the extremes of a continuum; Starrfelt & Kokko, 2012).

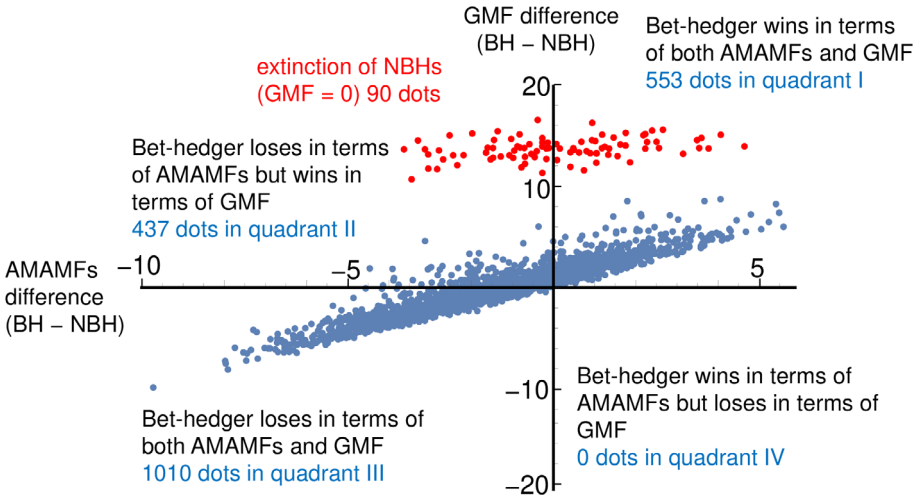



FIGURE 4 The relationship between the difference (diversified bet-hedging [DBH] minus non-bet-hedging [NBH] in this example) in arithmetic mean of arithmetic mean fitness (AMAMFs) across generations (*x*-axis) and that in the geometric mean fitness (GMF) across generations (*y*-axis). The positive values indicate that the bet-hedgers (BHs) beat the NBHs in each pairwise competition. Conditions in this example: iterations in the simulation (2000); no. of generations (10); no. of independent groups of the same genotype (synchronously fluctuating) in each generation (= degree of environmental grain) (2); no. of reproductive events per individual (5); original mean fitness of NBHs (Figure 2a) (15); and cost of bet-hedging (10% reduction in AMF). NBH extinction occurred in 90 out of 2000 iterations (red dots). No extinction occurred in DBHs [Color figure can be viewed at wileyonlinelibrary.com]

## 2.3 | Calculation of mean fitness

The AMF among mother groups employing the same strategy was calculated (Figure 3b). The more independent patches there were (= the finer-grained the environment; the larger the *evg*), the lower the BGV in AMF achieved was (the law of large numbers), even for NBHs (Table 4). Note that Figure 3a shows the distribution of IF, whereas Figure 3b shows that of the AMF for each genotype in a generation when $evg = 2$. In CBH and DBH, reduction of fitness variance has already been achieved in a single environment (Figure 3a) but occurs by the averaging across two environments in NBH (Figure 3b). Averaging between only two independent patches greatly reduces the reproductive failure of NBH.

Next, I conducted pairwise comparisons between NBHs and CBHs or DBHs (Figure 4). The same number ($evg = 1$–5, equivalent to the degree of environmental grain = the number of patches) of IF values ($x_1, x_2, ..., x_{evg}$) was randomly chosen from the IF distributions of NBH and CBH or DBH in Figure 3a, and the arithmetic mean was calculated for each genotype ($\text{AMF} = \frac{x_1+x_2+\cdots+x_{evg}}{evg}$; Figure 3b). This procedure was repeated $g$ times (for $g$ generations) for each strategy. For simplicity, the generations were discrete, and the arithmetic mean (AMAMF) and geometric mean (GMF) of AMFs across $g$ generations were calculated. Finally, the pairwise datasets of AMAMF differences (CBH or DBH – NBH) and GMF differences (CBH or DBH – NBH) were plotted (Figure 4) (2000 iterations of $g = 10$ generations). For various parameter ranges, that is, the number of independent patches in a population (environmental grain $evg = 1$–5), standard deviation of CBHs ($\sigma = 2$–10, compared to $\sigma = 10$ of NBHs), number of reproductive events per DBH individual (1–10) and cost of bet-hedging (0%–20% reduction in mean genotypic fitness compared to that of NBHs) were examined.

## 2.4 | Specialists (risk-prone strategies) in fine-grained environment

In Section 1.4, I hypothesized that in fine-grained environments (Figure 2b), in which the fitness correlation among individuals of the same genotype is low because each individual experience different environment, specialist (high-risk high-return) strategies could avoid extinction via the same mechanism as MLDBH. To test this idea, the probability of extinction (occurrence of GMF = 0) of NBH was evaluated under the conditions with various environmental grain ($evg = 1$–10) and fitness variance ($\sigma = 2$–30; from risk-averse to risk-prone) but constant IF ($\mu = 15$).

# 3 | RESULTS

## 3.1 | Evolution of bet-hedging

Figure 4 shows the relationship between the AMAMF difference and GMF difference (= BH – NBH). In certain

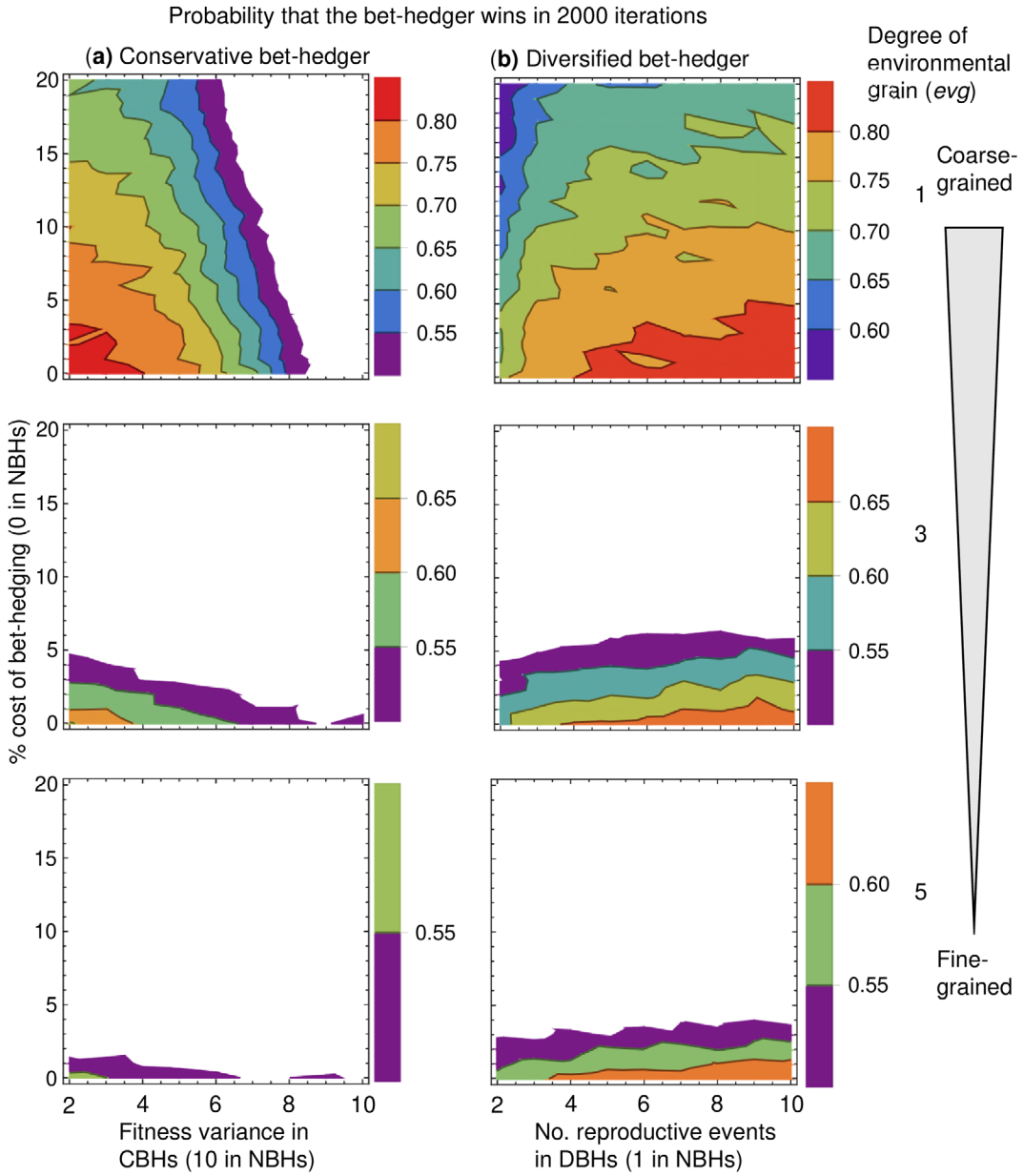



**FIGURE 5** The parameter ranges enabling bet-hedging evolution (a, conservative bet-hedging [CBH]; b, diversified bet-hedging [DBH]). The area of colored contours indicates that bet-hedgers (BHs) can increase in the population by outcompeting non-bet-hedgers (NBHs). The white plane means that NBHs win. Conditions: iterations in the simulation (2000); no. of generations (10); original mean fitness of the NBH genotype (Figure 2a) (15). Environmental grain (*evg*) is constant throughout generations. See the text [Color figure can be viewed at wileyonlinelibrary.com]

parameter sets, the GMF of bet-hedgers was greater than that of NBHs (the dots in Quadrants I and II in Figure 4). In particular, NBHs often went extinct because they drew 0 within 10 generations. On the other hand, CBHs and DBHs very rarely went extinct. This greatly increased the GMF differences (in the example of Figure 4, ca. 4.5% of dots concentrate around $y = 13.5$).

For the reason mentioned later (see Section 4.1), I considered the evolutionary condition of bet-hedging to be that the CBHs or DBHs win with a probability of 0.5 or more in terms of GMF (i.e., 50% or more dots in Quadrants I + II in Figure 4). I explored the parameter sets enabling this condition (Figures 5 and 6). In general, bet-hedging is evolvable if the fitness variance of CBHs is small or DBH mothers reproduce frequently and the potential fitness cost of bet-hedging is small (Figure 5). Repeated reproduction (Figure 5b) seemed more effective than variance reduction (Figure 5a) in increasing GMF. However, a bet-hedger is advantaged only in coarse-grained environments (small *evg*). This is because when only one or two independent patch(es) or mother group(s) of the same genotype existed in the population, the

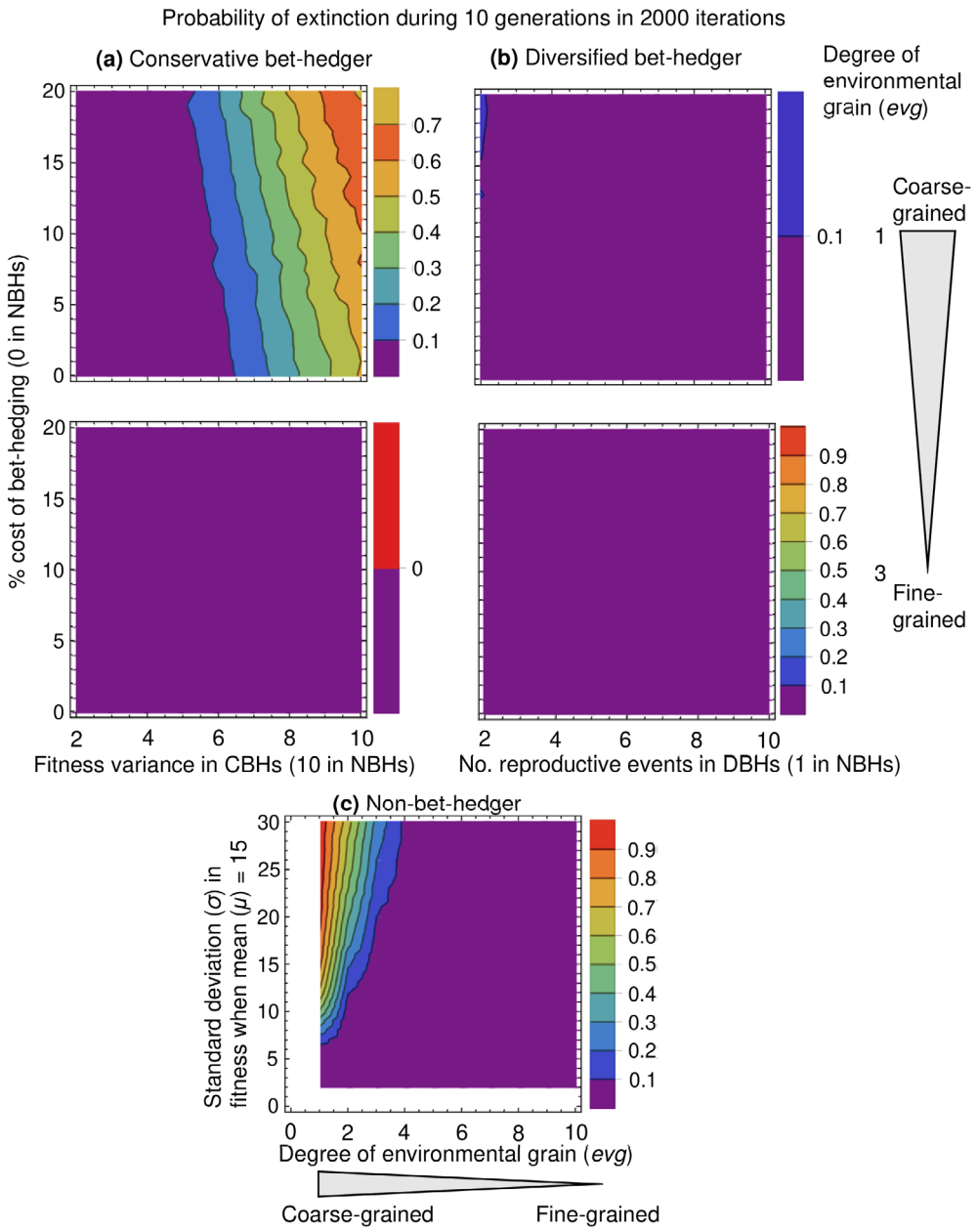



**FIGURE 6** The extinction probability of conservative bet-hedgers (CBHs) (a), diversified bet-hedgers (DBHs) (b) and non-bet-hedgers (NBHs) (c) under various parameter sets. The purple planes indicate no extinction. In fine-grained environments ($evg \geq 3$), no extinction occurred in CBHs and DBHs. Conditions: iterations in the simulation (2000); no. of generations (10); and original mean fitness of the NBH genotype (Figure 2a) (15). See the text [Color figure can be viewed at wileyonlinelibrary.com]

extinction (GMF = 0) of NBHs more frequently occurred than that of CBHs and DBHs, but if $evg \geq 3$, extinction no longer occurred for all strategies (Figure 6). NBHs win because BHs entail deterministic cost. However, even in a fine-grained environment ($evg = 5$), the BH strategies can evolve in a small (≤3%) cost range (Figure 5).

### 3.2 | Environmental grain and non-bet-hedging (specialist)

In the coarse-grained environments ($evg = 1$–$2$), the non-bet-hedging specialist genotype frequently went extinct if it took "risk-prone" strategies (higher fitness variances) (upper left area in Figure 6c). However, in the fine-grained environments ($evg > 4$), meaning several independent mother groups of the same genotype exist within the dispersal range, risk-prone strategies no longer went extinct (equally or more competitive compared to BHs).

## 4 | DISCUSSION

### 4.1 | The new meaning of the old definition

If the traditional definition (Philippi & Seger, 1989; Seger & Brockmann, 1987; Slatkin, 1974) treats a strategy as bet-hedging only when it "loses in terms of the arithmetic mean but wins in terms of the geometric mean" in

empirical studies, only the dots in Quadrant II in Figure 4 satisfy this requirement. If these dots are more frequent than 50% of the total 2000 dots (a winning percentage > 50%), this "bet-hedging in the strict sense" can increase (i.e., evolve) in a population. However, I could not find such a condition within the limited number of generations ($g = 10$ as a realistic range in experimental studies). Whenever many dots existed in Quadrant II, Quadrant I contained a comparable number of dots (Figure 4). Therefore, bet-hedging cannot evolve under this strict definition. Because the simulations did not incorporate any arbitrary assumptions other than a genotype-intrinsic trait value and its variance, this conclusion is very general and robust.

Instead, it is appropriate to relax the requirement and define it as winning in terms of the between-generation GMF (irrespective of the within-generation AMF; that is, 50% or more dots in Quadrants I + II of Figure 4). The simulations under this standard (Figures 5 and 6) show that bet-hedging is evolvable. Note that because bet-hedgers already paid potential costs at the genotypic level (the mean difference in Figure 3), the definition of an AMAMF-GMF trade-off is met even if it was not observed at the realized phenotypic level (Figure 4). This is analogous to condition-dependent handicap traits in sexual selection such as the peacock's tails (Johnstone, 1995; Zahavi, 1975). The high cost of such conspicuous ornaments is payable only for highly genetically conditioned males, and thus, ornaments can be a reliable indicator of male genetic quality (Andersson 1994). Likewise, the cost of bet-hedging is not a problem for good-condition individuals, and they exhibit high performance in terms of both the AMF and GMF (as Case 2 in Table 2). Therefore, the old definition itself is reasonable but it has been misinterpreted and misused, in turn underestimating the role of bet-hedging in biological evolution.

## 4.2 | Why do bet-hedgers win?

The selective advantage of bet-hedgers mainly comes from the frequent extinction of NBHs in coarse-grained environments (Figure 6). When only one group of mothers of the same genotype whose fitness scores are completely synchronized (= individuals in the same microenvironment) exists in the population, NBHs unavoidably experience 0 fitness at some point over generations, and the GMF becomes 0 (i.e., extinction occurs). Although bet-hedgers incur the cost, meaning that their fitness distribution (Figure 2) shifts toward 0, they can maintain a positive GMF. CBHs avoid extinction by suppressing their fitness variance itself. Because these bet-hedgers maintain a narrower fitness distribution (Figure 2) at all levels (within-generation and between-generation; Table 4), they draw 0 very rarely. DBHs also avoid extinction by (arithmetically) averaging the fitness fluctuation across multiple reproductive events within-individuals and across multiple individuals within generations (i.e., risk spreading). In each reproductive event of DBH, the potential fitness distribution is not different from that of NBHs, but the averaging recreates the narrower realized distribution (Figure 2) for DBHs. Thus, although DBHs draw 0 with the same probability as NBHs, they can compensate for it with other positive values $\left(\text{e.g.,, } \frac{10+0}{2} = 5\right)$.

## 4.3 | Fine-grained environments alter non-bet-hedgers into bet-hedgers

As predicted in Section 1.4, fine-grained environments favor NBH producing a single specialist phenotype. There, NBH is equally competitive to CBH or DBH. When $evg \geq 5$, five or more individuals of the same NBH genotype distribute over multiple patches with different conditions or experience different fitness-related events. Consequently, the probability that all NBH individuals unluckily fail reproduction is nearly zero even if they took a risk-prone strategy (large fitness variance such as $\sigma = 30$) (Figure 6c). Recently, several authors suggested that the risk-prone strategy could evolve in fine-grained environments (Haaland et al., 2019) or if extinction probability is very low and the fitness return is very high (Ito, 2019; Ito et al., 2013). The present results support this view. Thus, fine-grained environments alter NBHs into BHs. In other words, the adaptations to alter the environmental grain from coarse to fine, by distributing offspring at spaciotemporally wider range than the extent of environmental change are equivalent to bet-hedging.

## 4.4 | Rethinking bet-hedging: How to cope with unavoidable reproductive failures

Organisms face unpredictable environmental changes and every kind of uncertainty affecting their reproductive success (Hopper, 1999; Philippi & Seger, 1989; Slatkin, 1974). Bet-hedging can control uncertainty. One simple equation explains the essence of bet-hedging:

$$\frac{w_1 + w_2 + \cdots + w_f}{f} \geq \sqrt[f]{w_1 w_2 \ldots w_f}, \quad (1)$$

where $w_1, w_2, \ldots, w_f$ are the fitness scores of $f$ reproductive events of the same genotype (strategy).

Equation (1) shows the relationship between the arithmetic mean (left side) and geometric mean (right side), indicating that the arithmetic mean is larger than or equal to the geometric mean of the same sample set. It also indicates that when all samples have the same value ($w_1 = w_2 = \cdots = w_f$), the geometric mean coincides with the arithmetic mean, and they are simultaneously maximized.

However, variability in the fitness score itself is unavoidable in real cases, and thus, the multigenerational maintenance of the same score (even a moderate value) is impossible. Hence, maximizing GMF through CBH strategies is difficult in practical cases. If 0 fitness in a single reproductive event (within $w_1, w_2, \cdots, w_f$) occurs, the right side of Equation (1) becomes 0, but the left side does not. Therefore, a conversion from the situation where the mean fitness should be calculated as the geometric mean to the situation where the mean fitness can be calculated as the arithmetic mean, namely, the transfer of fitness variation from multigenerational events to within-generation events, is an effective strategy. This transfer should be called within-generation (but across multiple reproductive seasons or across multiple habitats) diversified bet-hedging (WGDBH in Table 1); each generation consists of $n$ individuals performing $f$ reproductive events and generation is repeated for $g$ times. The fitness scores including 0 are (arithmetically) averaged within generations and the resulting GMF across $g$ generations is almost always some positive value (unless all $w_{j,i,e}$ values are 0 in the same generation; this is possible but unlikely, because if all reproductions fail, no strategy can cope with it!), meaning long-term sustainability.

In WGDBH (Table 1, Figure 7b), we can see that the single $w_{j,i,e} = 0$ affects the entire GMF very little. Thus, the DBH strategy is generally more powerful than the CBH strategy because of the tolerance of 0 (Figure 5). The WGDBH provides a new conceptualization of bet-hedging in the context of biology. Specifically, bet-hedging is not a strategy for avoiding any reproductive failure (0 fitness) but rather a strategy for coping with unavoidable failures.

Organisms achieve WGDBH by making their environments fine-grained. They reproduce repeatedly over multiple seasons to make temporally fine-grained environments or move wider across habitats with different conditions to make spatially fine-grained environments (Figure 7). For these reasons, iteroparity (Hopper, 1999; Stearns, 1992) and dispersal or migration (metapopulation structure: Hanski, 1999; Levin, 1974; Marsh & Trenham, 2001) have evolved in many species. Both activities are costly in terms

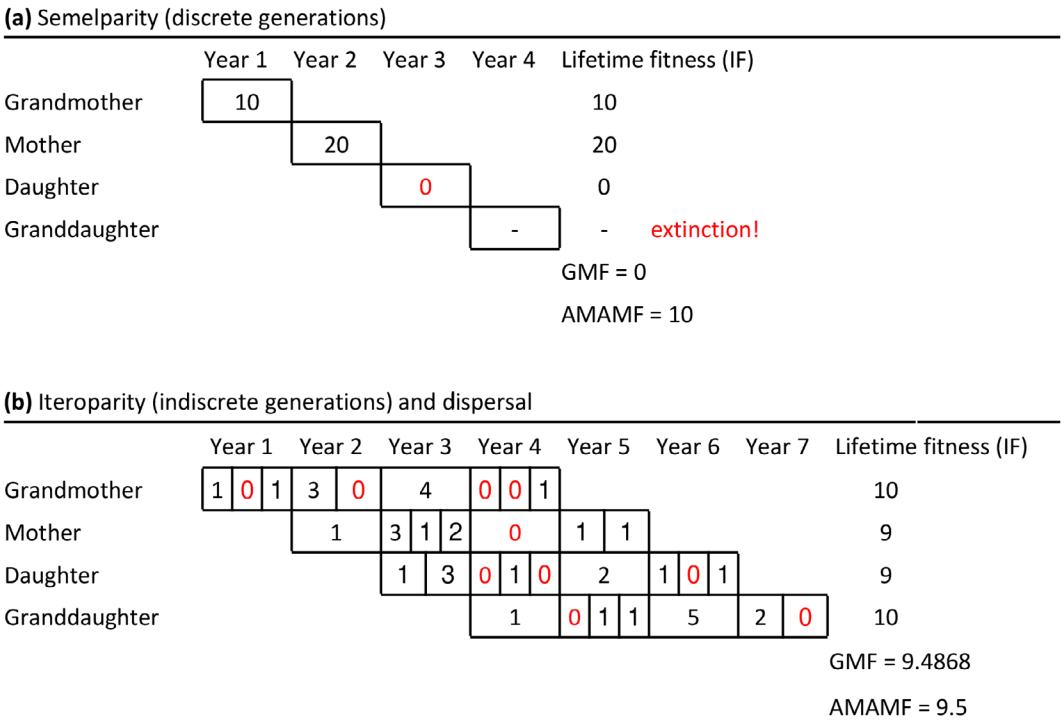



FIGURE 7 Within-generation diversified bet-hedging. Reproductive success of four generations of a single lineage is shown. (a) In semelparity and nondispersal, a single reproductive failure (0 fitness) leads the lineage to extinction (geometric mean fitness [GMF] = 0). (b) In iteroparity and dispersal across up to three habitats, zero values affect the entire GMF (sustainability) very little because of the risk-spreading over years or habitats (but within generations). The cost of bet-hedging appears as a reduction in the arithmetic mean of arithmetic mean fitness (AMAMF) in iteroparity and dispersal [Color figure can be viewed at wileyonlinelibrary.com]

of AMF (momentary rate of increase) but achieve high GMF. Thus, WGDBH also meets the trade-off definition of bet-hedging (Table 1). Large animals (e.g., mammals and birds) and perennial trees employ iteroparity, suggesting the significance of a large size and a long life. Short-lived organisms such as annual plants and *Daphnia* produce dormant seeds (Cohen, 1966) and resting eggs (Alekseev & Lampert, 2001), respectively. Although parents are annual, the offspring reproduce over multiple seasons (thus, the situation is temporally fine-grained). Almost all organisms disperse offspring over multiple places with different environments or different luck. They change environment into spatially fine-grained. Some offspring enter good habitats (e.g., suitable climate) or meet good luck (e.g., escaping from predation). According to the classification of Hopper (1999), the former and latter correspond to "metapopulation bet-hedging" and "within-generation bet-hedging," respectively. Both strategies are based on the same logic but the NBH to which these strategies are compared (as controls) are different with regard to environmental grain: the NBH compared to metapopulation bet-hedging is confined within a single environmental type but the NBH compared to within-generation bet-hedging moves across environments (in other words, the latter is equivalent to MLDBH). Such a complicated classification of bet-hedging has now been disentangled.

Most importantly, the existence of multiple individuals with the same strategy in the population offsets the fitness fluctuation among individuals. Indeed, reproduction is an activity for making spare individuals of the same genotype. Because spare individuals belong to different circumstances (fine-grained environments), the genotype can avoid being ruined altogether. Therefore, reproduction itself is bet-hedging (Yasui & Yamamoto, 2021). Against what?—Non-reproduction. Does it cost?—Yes. Reproducing individuals reduce their own survival rate compared to that of non-reproducers but increase their long-term persistence, where the cost of bet-hedging is integrated into the general cost of reproduction (Stearns, 1992).

## 5 | CONCLUSIONS

This study dissects the complicated logic and structure of bet-hedging. The mean–variance trade-off is simply an assumption that should be tested (Yasui & Yamamoto, 2021). The negative correlation (trade-off) between within-generation AMF and between-generation GMF is not a necessary condition for confirming bet-hedging in empirical studies. I reorganized the definition of bet-hedging and expanded its meaning. If a mother successfully distributes offspring over the range covering all possible spaciotemporal environmental conditions (making fine-grained environments), reproductions at multiple places and in multiple seasons become single-generational events (Figure 7b). Because within-generation fitness is calculated as arithmetic mean (AMF), it can offset fitness fluctuation (occurrence of 0). Organisms are entities that reproduce, and reproduction itself is bet-hedging. Therefore, bet-hedging is a ubiquitous, universal law of biology.

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## CONFLICT OF INTEREST

The author declares no potential conflict of interest.

## DATA AVAILABILITY STATEMENT

The codes of the simulations are provided as supporting information.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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