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Bet-hedging—a triple trade-off between means, variances and correlations

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ABSTRACT

In unpredictably varying environments, strategies that have a reduced variance in fitness can invade a population consisting of individuals that on average do better. Such strategies 'hedge their evolutionary bets' against the variability of the environment. The idea of bet-hedging arises from the fact that appropriate measure of long-term fitness is sensitive to variance, leading to the potential for strategies with a reduced mean fitness to invade and increase in frequency. Our aim is to review the conceptual foundation of bet-hedging as a mechanism that influences short- and long-term evolutionary processes. We do so by presenting a general model showing how evolutionary changes are affected by variance in fitness and how genotypic variance in fitness can be separated into variance in fitness at the level of the individuals and correlations in fitness among them. By breaking down genotypic fitness variance in this way the traditional divisions between conservative and diversified strategies are more easily intuited, and it is also shown that this division can be considered a false dichotomy, and is better viewed as two extreme points on a continuum. The model also sheds light on the ideas of within- and between-generation bet-hedging, which can also be generalized to be seen as two ends of a different continuum. We use a simple example to illustrate the virtues of our general model, as well as discuss the implications for systems where bet-hedging has been invoked as an explanation.

Key words: bet-hedging, environmental variability, fitness, diversification, uncertainty.

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I. INTRODUCTION

Individual organisms face a variety of challenges during their lifetime: risks of predation, mortality due to unfavourable conditions, and variability in availability of resources among many others. Many of these challenges are unpredictable. To be able to survive and reproduce, individuals often need to exhibit adaptations that respond to the diversity of conditions of life that they may encounter. When there is a predictable relationship between a signal and fitness consequences, we expect phenotypic plasticity to evolve (Pigliucci, 2001). When they cannot be measured or predicted in advance, lineages of individuals can increase in frequency if genotypes 'hedge their bets' (Slatkin, 1974) or 'spread the risk' (den Boer, 1968). Loosely speaking, bet-hedging is beneficial because it avoids worst-case scenarios such as a lineage of wet-adapted individuals dying because of a rare dry year; if the best genotype in the wet year always dies out during a drought it cannot prevail in the long run. More precisely, a successful lineage must survive and reproduce over a wider range of environmental conditions than experienced by individual organisms (including conditions that change over longer periods of time than a generation). Arithmetic mean fitness across environments, often used to describe reproductive success at the level of the individual, is then not a sufficient measure. In uncertain environments we expect adaptations that make individuals not maximize their expected fitness, instead; evolutionary predictions cannot be made without taking into account the variance in fitness.

Our aim is to review the conceptual foundation of bet-hedging as a mechanism that influences short- and long-term evolutionary processes. The concept is based on metaphors that have not always invoked the clearest thinking, and we comment on some of these pitfalls. We will outline the different contexts in which the concept is used and explore their mathematical and conceptual relationships. Importantly, we will point out that bet-hedging is not a simple trade-off between the mean and the variance of offspring production. Instead, there are three factors whose interplay determines whether bet-hedging works: the arithmetic mean, the expected variance for an individual, and correlations in fitness among individuals, all measuring aspects of reproductive success for a lineage. Bet-hedging can bring about a benefit *via* any combination of the latter factors, at the expense of the first.

(1) What is bet-hedging? Metaphors and core ideas

"Don't put all your eggs in one basket" is a common idiom, with roots dating back to the 1700s (Ammer, 1992). The saying clearly advises against investing all one's assets in a single line of effort. It is clear that uncertainty is needed for this to make sense; otherwise one should put all the eggs in the same, best-performing basket (or investment fund). In evolutionary biology, an easy interpretation of this metaphor is that strategies that literally spread eggs into different nests will be favoured, perhaps because some nests fail completely while others survive, and it cannot be predicted in advance which will do so. However, is such 'insurance against nest failure' (Byrne & Keogh, 2009) really bet-hedging?

Bet-hedging in evolutionary biology is usually defined as a strategy or allele that increases the probability of its fixation by lowering the variance of fitness even though mean (arithmetic) fitness declines (Slatkin, 1974; Seger & Brockmann, 1987; Philippi & Seger, 1989). In the simplest case, consider a mother that lays two eggs, either in the same nest or in two different ones. Each nest may flood (or in the case of a frog, dry out), and all offspring in that nest then die. There is no density dependence within a nest, nor do we assume any reasons related to nest building or care that might make it less efficient to raise offspring in two different nests.

If flooding events are independent (hitting each nest with probability 0.5), then both strategies bring about the expectation of one surviving offspring, but the 'same-nest' mother will have either 0 or 2 surviving young, while the 'different-nest' mother may produce 0 (with probability 0.25), 1 (probability 0.5), or 2 (probability 0.25). Taking the metaphor at face value, it tells us that the latter genotype—that creates the mean 1 with a smaller variance—should win over time. In this review we will examine where, mathematically speaking, such a benefit could come about. First, however, it is worth noting that in the above oft-used example the variance is reduced but the arithmetic mean is unchanged. A strict definition of bet-hedging states that the bet-hedger should have paid a cost of a reduced mean. This is not mere nit-picking. In the empirical example of Byrne & Keogh (2009), polyandrous frogs that spawned in different nests had a higher mean offspring count, and bet-hedging is not really needed as the main explanation of why females mated multiply. We will explain below why, if predation risk is independent across nests, even very small costs of reduced mean arithmetic fitness may make bet-hedging not favour the multiple-nest mother.

"A bird in the hand is worth two in the bush" is another related idiom, originating in one of Aesop's fables (Ammer, 1992); "I should indeed be a very simple fellow if, for the chance of a greater uncertain profit, I were to forego my present certain gain" (Aesop, 2004, p. 56). The usual interpretation is that we have one thing of value in our possession already, and it might not be worth sacrificing that for the chance of getting something better (asset-protection principle; Clark, 1994). If one extends the meaning such that the contrast is not between something already gained *versus* something greater that may be possible to gain, but instead

between a sure fitness payoff and an unsure one (without any assumption about a temporal order that one has been gained already), it also works as a metaphor for bet-hedging. As we will explain below, this metaphor refers to a slightly different kind of bet-hedging than the 'eggs in a basket' metaphor.

(2) A standard example: temporally varying rainfall

Seger & Brockmann (1987) (see also Philippi & Seger, 1989) presented a thought-provoking example to which we will return numerous times throughout our review. Assume that the environment can be either wet or dry during a generation (e.g. a year for an annual plant). We consider four different genotypes: a drought-resistant genotype which forms the dry-year specialist (A_{dry}), a wet-year specialist (A_{wet}), a generalist (A_{gen}, also called a conservative bet-hedger), and finally a diversified genotype which gives rise to both wet year and dry year specialists (A_{div}, called a diversified bet-hedger). None of these can alter their development depending on the environment they grow in; instead, individuals with the A_{div} genotype develop into the wet- or dry-year specialist morph with a fixed probability irrespective of the environmental conditions. We assume haploid and asexual inheritance for simplicity, thus A_{div} offspring are again A_{div} and can phenotypically differ from their mother as they develop independently.

Table 1 lists the reproductive success of individuals of each genotype in wet or dry years; for an annual organism this is equivalent with fitness. The fitnesses in Table 1 are interpreted as absolute fitness of an individual (scaled by some constant). For our plant interpretation, a constant of 100 means that a plant of genotype A_{dry} will produce 100 seed of the same genotype in a dry year and 58 seed in a wet year.

Note that we assume that the generalist does reasonably well regardless of environmental conditions, but on average worse than either of the specialists. The diversified strategy's fitness values are obtained by assuming that the dry-year morph is produced with a probability 0.44 (see Section II.3 for the relaxing of this particular assumption).

In this set-up where there is temporal but no spatial variability in the environment, i.e. all individuals experience either a wet or a dry year, the strategy with the highest geometric mean fitness will eventually prevail (Dempster, 1955; Levins, 1968; Lewontin & Cohen, 1969; Seger & Brockmann, 1987; King & Masel, 2007). Thus, even though genotype A_{gen} has a lower arithmetic mean fitness, it will invade and replace both a population of A_{dry} and a population of A_{wet}. The generalist A_{gen} is often called a 'conservative' bet-hedger because its success is a result of giving up high success in any year and instead avoiding very poor success in any year. In other words, it fulfils the definition of bet-hedging since a reduction in mean arithmetic fitness is accompanied by a reduction in the genotypic variance in fitness (for this genotype this variance is 0). This lifts its geometric mean fitness above either A_{dry} or A_{wet} (see Section II.1*e* for the relationship between arithmetic and geometric mean fitness).

The generalist genotype is, however, not the best possible bet-hedger in this example. The last genotype (A_{div}) will invade and replace any population consisting of the other three genotypes. This genotype employs a diversified strategy, because it achieves a reduced genotypic variance in fitness by producing both wet-year and dry-year specialists within the same year. Depending on the circumstances, one or the other type will be highly productive, and there is never a year where the genotype does universally badly. This genotype therefore ends up with a higher geometric mean fitness than any of the other genotypes.

II. THE MATHEMATICS OF BET-HEDGING

The ideas of bet-hedging grew out of the appreciation of treating fitness as a random variable. The fitness of genotypes and individuals is not known in advance, but it can be described by a probability distribution. In our rainfall example above, the fitness of genotype A_{wet} can be described by its fitnesses achieved in dry and wet years, and the associated environmentally determined probabilities (i.e. the probability of a year being dry is $P = ½$). Treating fitness as a random variable complicates predictions of both short-term and long-term changes in allele frequencies. The general model in the next section is based largely on Frank & Slatkin (1990) and derivations of Rice (2008).

(1) Working towards the two advantages of bet-hedging: reduced individual fitness variance and reduced fitness correlation between individuals

Evolutionary models may predict how frequencies of alleles change over time or determine which alleles will go to

Table 1. The genotypic absolute fitnesses in the rainfall model, where the environment in a given year is either dry or wet

	Genotype			
	A_{dry}	A_{wet}	A_{gen}	A_{div}
Dry, $P_{dry} = ½$	1	0.6	0.785	0.776
Wet, $P_{wet} = ½$	0.58	1	0.785	0.815
Arithmetic mean fitness (expected fitness, μ)	0.79	0.8	0.785	0.796
Geometric mean fitness	0.762	0.775	0.785	0.795

A_{dry} is a dry-year specialist, A_{wet} a wet-year specialist, A_{gen} a generalist and A_{div} a diversified genotype that produces the dry-year phenotype with probability 0.44. For the calculation of the fitnesses of the diversified genotype see Section II.3. All references to properties of these genotypes are used with subscripts as here.

fixation. In a sense, the latter goal is a subset of the former, since fixation is a particular type of change over time. Nevertheless, the former goal is more directly related to detecting ongoing natural selection in empirical systems, whereas the latter is more related to developing ideas of optimality—trying to predict what kinds of behaviour or strategies we generally expect as a result of evolution, the alternatives having been weeded out by natural selection. Here we are interested in both approaches, as they differ in which concepts or measures of fitness to use (see e.g. Lande, 2007, for some confusion surrounding this). In line with the 'subset' thinking above, we will first describe the short-term changes and then proceed to extracting a fitness measure that can be used for long-term predictions. If bet-hedging is seen as the idea that evolution "proceed[s] *via* a trade-off between the expected value and the variance of fitness" (Childs, Metcalf & Rees, 2010, p. 3056), then this will be reflected in both short-term and long-term evolutionary predictions.

Genotypic fitness can be described as the mean fitness of all individuals of that genotype plus genotypic fitness variance around this mean. We will proceed by breaking this genotypic fitness variance down into two parts, variance at the level of the individuals and correlations among these individuals. This set-up helps to clarify the concepts of within- and between-generation bet-hedging (Gillespie, 1974*a*, 1975; Hopper, 1999) as well as conservative and diversifying bet-hedging (Seger & Brockmann, 1987; Philippi & Seger, 1989). As before, we assume asexual haploid females.

(*a*) *Short-term predictions*

We consider a population of size N consisting of haploid individuals carrying alleles A_1 and A_2 with respective frequencies of q_1 and q_2 (these could correspond to A_{wet} and A_{dry} in our drought example). To arrive at a model of frequency change we first write the genotypic mean fitness (R_i) in a given generation (which is the mean of the absolute fitness of individuals of a given genotype), i.e.

$$R_1 = \frac{1}{Nq_1}\sum_{j=1}^{Nq_1}(\mu_1 + \alpha_{1,j}) = \mu_1 + \bar{\alpha}_1, \tag{1}$$

$$R_2 = \frac{1}{Nq_2}\sum_{j=1}^{Nq_2}(\mu_2 + \alpha_{2,j}) = \mu_2 + \bar{\alpha}_2. \tag{2}$$

Here μ_1 and μ_2 are the expected absolute fitnesses (i.e. the arithmetic mean) of an individual of genotype A_1 and A_2, respectively. In addition $\alpha_{i,j}$ denote the individual deviances from this expectation within a particular generation, and these random variables are assumed to have a (global) mean of 0 and a variance of σ_i^2. In general we think of these deviations arising from different conditions experienced during the life of individuals. The expectations [μ_i and $\mathbb{E}(\alpha_{i,j})$, where $\mathbb{E}$ denotes expectation, most easily thought of as an arithmetic mean] are then calculated across all possible environments. Note, however, that for a given year $\bar{\alpha}_t$ need not be 0.

It follows that the expression for the average reproductive success in the whole population is given by

$$\overline{R} = q_1R_1 + q_2R_2. \tag{3}$$

Assuming non-overlapping generations we get the frequency of allele A_1 after one generation;

$$q_1' = q_1\mathbb{E}\left[\frac{R_1}{\bar{R}}\right]. \tag{4}$$

Since reproductive successes are random variables, allele frequencies and their changes also become random variables. The expected change in the frequency of allele A_1, given its present frequency, is

$$\mathbb{E}[\Delta q_1|q_1] = \mathbb{E}[q_1'|q_1] - q_1 = \mathbb{E}\left[\frac{q_1R_1}{\bar{R}}\right] - q_1 = \mathbb{E}\left[\frac{q_1q_2(R_1 - R_2)}{\bar{R}}\right]. \tag{5}$$

Dealing with the expectation of a ratio of random variables (as the one in the expectation above) can be difficult, but with some assumptions we can expand this expectation as a series. This is done by Gillespie (1974*a*, 1975), Frank & Slatkin (1990) as well as others (Shpak, 2005; Shpak & Proulx, 2007; Rice, 2008; Rice & Papadopoulos, 2009), and we refer to Appendix 1 for a more complete and easily accessible derivation of this general model. Because the concepts of bet-hedging refer to the first two moments of the series, we follow this general research tradition and focus our attention to the first two terms of the expansion. This means that the following only holds approximately (for extensive discussion of higher moments see Rice, 2008).

$$\mathbb{E}[\Delta q_1|q_1] = \mathbb{E}\left[\frac{q_1q_2(R_1 - R_2)}{q_1R_1 + q_2R_2}\right] \approx \frac{\mathbb{E}[q_1q_2\,(R_1 - R_2)]}{\mathbb{E}[q_1R_1 + q_2R_2]} + \frac{q_1q_2\,(q_2\,Var(R_2) - q_1\,Var(R_1) + (q_1 - q_2)Cov(R_1, R_2))}{\mathbb{E}[q_1R_1 + q_2R_2]^2}. \tag{6}$$

The first term is the expected change excluding any variation in the reproductive successes. This term is directly proportional to the difference in mean reproductive success of the two genotypes. The second part takes into account the variance of the genotypic successes. We continue by making the assumption that the average reproductive success for the whole population is close to 1 (i.e. that $\mathbb{E}[q_1R_1 + q_2R_2] \approx 1$). In addition we also observe that we can express the variance and covariance terms in Equation 6 as

$$Var(R_1) = \rho_1\sigma_1^2, \tag{7}$$

$$Var(R_2) = \rho_2\sigma_2^2, \tag{8}$$

$$Cov(R_1, R_2) = \rho_{12}\sigma_1\sigma_2, \tag{9}$$

where the ρ_i denotes the correlation in the fitness (reproductive success) of two randomly chosen individuals

from the same year, measured across several years. ρ_1 refers to this correlation when both individuals are of genotype A_1, ρ_2 to the correlation when both are of genotype A_2, and ρ_{12} to the correlation observed when one is A_1 and the other A_2. If all the individuals of these sets (e.g. a particular genotype) have the same reproductive success within years, this correlation is 1 (temporal variation is obviously required for to this to be measurable: for example, individuals of the drought-adapted genotype (A_{dry}) all perform well in dry years and badly in wet years).

We can then write the expected change in the frequency of allele A_1 as:

$$\mathbb{E}[\Delta q_1|q_1] = q_1 q_2\{(\mu_1 - \mu_2) + (q_2\rho_2\sigma_2^2 - q_1\rho_1\sigma_1^2 + (q_1 - q_2)\rho_{12}\sigma_1\sigma_2)\}. \quad (10)$$

This is an approximation, and therefore will not hold exactly for a wide range of models, but it is very useful as a heuristic; we will exemplify it by returning explicitly to our rainfall model. Also note that often models can be transformed to fit the assumptions of this approximation.

In Equation 10, the expected direction and magnitude of change is affected by three terms: the expected genotypic fitnesses (arithmetic across all environments, which is also the individual mean fitness, μ_i), the variances in reproductive success at the individual level (σ_i^2) and the correlation of reproductive success between individuals (ρ_i). This is an important insight because a reduction in mean fitness can be compensated by changes in either of these latter two terms, and these have a direct relationship to the different types of bet-hedging.

One consequence of fitness as a random variable is that it creates 'implicit' frequency dependence that, as a net effect, favours consistently performing genotypes (Seger & Brockmann, 1987; Frank & Slatkin, 1990; Lande, 2007). As we have seen above, the genotypic variance of an allele affects the evolutionary dynamics, and this happens more strongly for abundant alleles ($\rho_i \times \sigma_i^2$ is multiplied by the frequency q_i). To see where the importance of this variability in absolute fitness comes about, we now turn to Jensen's inequality and the mathematical relationship between absolute and relative fitness.

(b) *Jensen's inequality*

Jensen's inequality is a general statement that relates the values of a concave function of an integral to the integral of a concave function. This has important consequences for expectations of random variables, since the integral of a probability distribution is by definition the expectation of a random variable. In Fig. 1 $F(X)$ is a concave function of X. If X is distributed with some deviation around a mean value μ then a downwards deviation in X decreases in $F(X)$ more than an equally large increase in X increases $F(X)$. As a result, the expected value of $F(X)$ will be less than the expected value of $F(X)$ evaluated at the mean value of X, $F(\mathbb{E}[X]) = F(\mu)$:

$$\mathbb{E}[F(X)] \leq F(\mathbb{E}[X]). \quad (11)$$

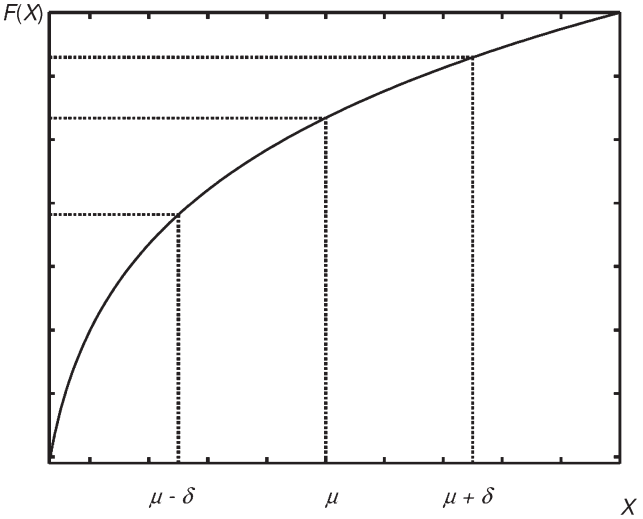

Fig. 1. Illustration of Jensen's inequality. For a variable X with mean μ, the negative deviations affect the mean of $F(X)$ more (negatively, y-axis) than positive deviations.

With regards to bet-hedging, there are two different types of concave functions that are invoked on a distribution of absolute fitnesses: the function mapping absolute fitness to relative fitness and the function mapping absolute fitness to geometric mean fitness. The first is important in making short-term predictions, the second in long-term predictions.

(c) *Absolute genotypic fitness to relative fitness*

By relative fitness we refer to a genotype's fitness divided by the population mean fitness. The relative fitness of allele A_1 in a haploid system with two alleles (A_1 and A_2) is given by

$$W_{1,\text{rel}} = \frac{R_1}{q_1 R_1 + q_2 R_2} \quad (12)$$

which is a concave function of R_1, with $q_2 = 1 - q_1$. If we assume that the absolute fitness of A_2 (R_2) is 1, a higher R_1 brings about a higher relative fitness for A_1, but the shape of this function depends on the frequency of the allele A_1 (Fig. 2). When allele A_1 is rare (low q_1), the relationship between R_1 and relative fitness is almost linear. On the other hand, as its frequency increases, the relationship becomes increasingly concave: even if the absolute fitness of A_1 happened to be vastly superior to A_2, it is hard to outcompete everyone else (required for achieving good relative fitness) when most others have the superior allele A_1 as well. In such a case, if there is variation in R_1, negative deviations from its mean reduce relative fitness more than positive deviations increase it. This is what leads to the implicit frequency dependence of the importance of variance in genotypic fitness (Equation 10, see Fig. 3).

(d) *Long-term predictions*

Does the implicit frequency dependence matter in the long term? If the expected change in the frequency of an allele is

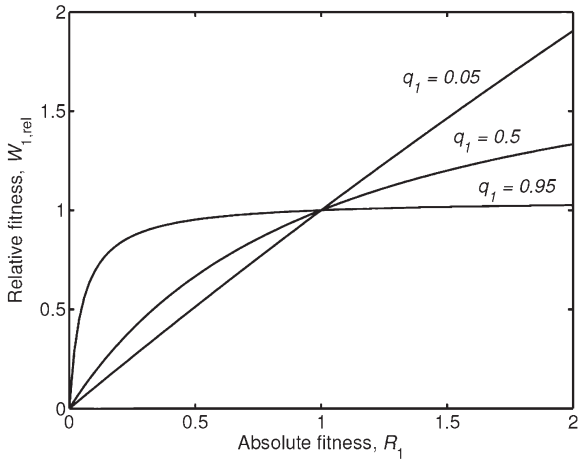

Fig. 2. The map from absolute (R_1) to relative fitnesses ($W_{1,\mathrm{rel}}$) for different frequencies of allele 1. The concavity of the map from absolute to relative fitness depends on the frequency of an allele. Here we have assumed that one allele (with frequency $q_2 = 1 - q_1$) has fixed fitness R_2 at 1. The fact that the genotypic fitness variance of an allele affects the evolutionary dynamics (Equation 10) scaled by its frequency, comes about because of this; for very low frequencies the map is almost linear, and then the variance in absolute fitness does not have a disproportionate effect on the relative fitness.

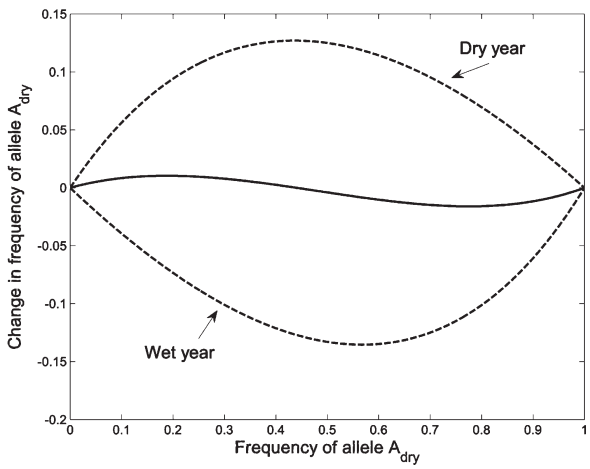

Fig. 3. The expected change in the frequency ($\mathbb{E}[\Delta q_{\mathrm{dry}}|q_{\mathrm{dry}}]$, Equation 10) of the dry-year-specialist allele (A_{dry}) in competition with the wet-year specialist (A_{wet}) for all frequencies of A_{dry} (x-axis). We see clearly that the expected change exhibits implicit frequency dependence (for $q_{\mathrm{dry}} > 0.44$ the expected change is negative, while for $q_{\mathrm{dry}} < 0.44$ it is positive). In addition we have plotted the exact changes in dry and wet years; if years are always dry the allele will always increase.

positive (or negative) across all frequencies (i.e. if Equation 10 does not change sign between frequencies 0 and 1), the allele will be fixed at frequency 1 (or 0). Deriving the long-term prediction is then fairly straightforward. However, things are not as simple when the expected change in the frequency of an allele changes sign depending on the current frequency (Frank & Slatkin, 1990, see also Fig. 3). If we assume infinitely large population sizes and a well-mixed population, the geometric mean genotypic fitness determines which allele goes to fixation (Dempster, 1955; Levins, 1968; Lewontin & Cohen, 1969; Frank & Slatkin, 1990; Lande, 2007).

(e) *Absolute genotypic fitness to geometric mean fitness*

The geometric mean of a series of n random variables ($R_{1,y}$) can be written as

$$G = \left(\prod_{y=1}^{n} R_{1,\mathrm{y}}\right)^{1/n} = \sqrt[n]{R_{1,1}R_{1,2}\cdots R_{1,n}}$$

$$= \exp\left(\frac{1}{n}\sum_{y=1}^{n}\ln(R_{1,y})\right) = \exp\ (\mathbb{E}[\ln(R_{1,y})]). \qquad (13)$$

The geometric mean is the nth root of the product of a series of n fitness values, but it can also be written as the exponential of the arithmetic mean log fitness. This is where Jensen's inequality comes into play. Logarithms are concave functions, and since the last term in (Equation 13) is the expectation of a log-transformed variable, the negative deviances in $R_{1,\mathrm{y}}$ will decrease the geometric mean more than positive deviances will increase it.

We can approximate the geometric mean fitness of a genotype/allele using the first two moments (i.e. the mean and variance) of the distribution of the absolute genotypic fitnesses, if we assume that the deviances ($\delta_{\mathrm{Geno,y}}$) are small (variance σ^2_{Geno}) and denoting the arithmetic mean fitness as μ_{Geno} (note that the subscript Geno refers to measures at the level of the genotype and not the individual level, i.e. σ^2_{Geno} is the genotypic fitness variance).

$$\mathbb{E}[\ln(R_{Geno,y})] = \mathbb{E}\left[\ln\left(\mu_{Geno}\left(1+\frac{\delta_{Geno,y}}{\mu_{Geno}}\right)\right)\right]$$

$$= \mathbb{E}[\ln(\mu_{Geno})] + \mathbb{E}\left[\ln\left(1+\frac{\delta_{Geno,y}}{\mu_{Geno}}\right)\right]. \qquad (14)$$

Then using the expansion ($\ln(1+x) = x - x^2/2 + \cdots$) on the second term above gives

$$\mathbb{E}\left[\ln\left(1+\frac{\delta_{Geno,y}}{\mu_{Geno}}\right)\right]$$

$$= \mathbb{E}\left[\frac{\delta_{Geno,y}}{\mu_{Geno}} - \frac{1}{2}\left(\frac{\delta_{Geno,y}}{\mu_{Geno}}\right)^2 + \cdots\right] \approx -\frac{\sigma^2_{Geno}}{2\mu^2_{Geno}}, \qquad (15)$$

while noting that $e^x = 1 + x + x^2/2 + \cdots$

$$G \approx \exp\left(\mathbb{E}[\ln(\mu_{Geno})] + \mathbb{E}\left[\frac{\delta_{Geno,y}}{\mu_{Geno}} - \left(\frac{\delta_{Geno,y}}{\mu_{Geno}}\right)^2 + \cdots\right]\right)$$

$$= \mu_{Geno}\left(1 - \frac{\sigma^2_{Geno}}{2\mu^2_{Geno}}\right) = \mu_{Geno} - \frac{\sigma^2_{Geno}}{2\mu_{Geno}} \qquad (16)$$

gives the commonly used approximation for the geometric mean. It is now obvious that increasing the variance in the

absolute fitness values of a genotype will decrease the geometric mean. It is important to realize that the variance above (σ^2_{Geno}) refers to genotypic variance, which in our framework is the product of between-individual correlation (ρ_i) and the individual-level variance (σ_i^2 in Equations 7 and 8). In the case of full correlation (i.e. no difference in fitness between individuals within the same year, $\rho_i = 1$), these have the same value.

The geometric mean fitness of an allele can then be approximated by

$$G_i = \mu_i - \frac{Var(R_i)}{2\mu_i} = \mu_i - \frac{\rho_i \sigma_i^2}{2\mu_i}. \quad (17)$$

This is a recapitulation of the principle (Equation 10) that the success of a strategy depends on the mean arithmetic fitness, on the individual variance in reproductive success, and on the correlation between individuals.

However, Equation 17 itself is an approximation. When the population sizes are finite (and particularly small), then it is not correct to state that the geometric mean predicts the fixation of an allele (Gillespie, 1974*a*; Frank & Slatkin, 1990; Proulx & Day, 2001). For instance, if fitnesses for individuals of a genotype are independent in a finite population (giving an average correlation of $\rho_i = 1/q_i N$) the condition for fixation of allele 1 is (Gillespie, 1974*a*; Frank & Slatkin, 1990)

$$\mu_1 - \frac{\sigma_1^2}{N} > \mu_2 - \frac{\sigma_2^2}{N}. \quad (18)$$

This differs from the geometric mean fitness, contrary to common belief (as held by e.g. Hopper, 1999; Hopper *et al.*, 2003), which in this case is approximately $G_i \approx \mu_i - \sigma_i^2/2N\mu_i$. As population sizes become larger, the effect of individual-level variance decreases in both cases, and for infinitely large population sizes, the geometric mean (and Equation 18) is identical to the arithmetic mean for uncorrelated fitness values among individuals (see Appendix 1).

To return to our initial example of eggs in flooding nests: in large, well-mixed populations it does not matter whether a mother lays her eggs in one or two nests. Natural selection in this case has a large enough sample size to 'see' that failing nests produced by the 'all eggs in one basket' genotype are exactly compensated by an equally large number of successful nests. The need to spread the risk disappears as the worst-case scenario where all nests fail (for a whole genotype) becomes exceedingly improbable due to the sheer number of nesting attempts. Mathematically, the effect of variation in nest success becomes insignificant in this case because the number of individuals is very large. Even a small cost of building and maintaining multiple nests would then be sufficient for bet-hedging to be selected against, or conversely, if there are direct benefits to using multiple nests these will dominate [e.g. in the context of conspecific brood parasitism, Pöysä & Pesonen (2007) show that conspecific brood parasitism evolves much more easily if it increases offspring survival *via* assessment of nest-specific predation risk, than if eggs are laid randomly]. This argument also makes it doubtful that bet-hedging alone works as a sole explanation for multiple mating, if it is associated with any costs, since each female will 'sample' the distribution of male quality independently [for a detailed investigation of this in the context of fertility insurance, see Hasson & Stone (2009) and Yasui (2001)].

(2) Returning to the dry and wet year example

Equation 10 yields a number of observations for our rainfall example. First, comparing the two specialists A_{dry} and A_{wet}, their expected fitness reaches the values $\mu_{dry} = 0.79$ and $\mu_{wet} = 0.80$. The between-individual correlations are $\rho_{dry} = 1$ for individuals with allele A_{dry}, and $\rho_{wet} = 1$ for genotype A_{wet}, since within a year all individuals have the same fitness, but it varies among years.

We can now see the implicit frequency dependence of the success of genotypes (Fig. 3) by plotting the expected change (Equation 10) in the frequency of A_{dry} against its current frequency in a population consisting of specialists only (A_{wet} and A_{dry}). Even though the model incorporates no change in arithmetic (or geometric) mean fitness that depends on the genotypes of the competitors, the expected change is not independent of frequency, due to the variance terms in Equation 10. Note that the correlation between individuals of the alleles A_{dry} and A_{wet} (ρ_{12}) is -1, since the conditions that predict high fitness for the dry-adapted genotype also predict low fitness for the wet-adapted one, and *vice versa*.

(3) Conservative *versus* diversified bet-hedging

Expressing the variance in genotypic fitness as a function that increases with the correlation between individuals as well as with the variance in individual reproductive success (equation 7–9) gives a clear theoretical underpinning for the differences between conservative and diversified bet-hedging strategies. In the case of the generalist strategy A_{gen}, the genotypic variance, $var(R_{gen})$, is reduced, as individuals always do reasonably well regardless of circumstances (small individual-level variance σ^2_{gen} in Equation 7). This is a clear case of the 'bird in the hand' metaphor, which makes the term 'conservative bet-hedging strategy' appropriate (Seger & Brockmann, 1987; Philippi & Seger, 1989). The A_{div} allele achieves the reduction in the genotypic variance in a different way. This bet-hedger largely fails to reduce the variance of individual fitness, as individuals of genotype A_{div} experience almost the same variance in individual success as genotypes A_{wet} and A_{dry}. The majority of the reduction of genotypic variance of the A_{div} allele is instead achieved by reducing the correlation (ρ_{div}) of reproductive success between individuals who share the same allele. Two randomly picked A_{div} individuals will not all have the same reproductive success within a year: some will have developed drought resistance, while others will have opted for the wet-adapted phenotype. This example follows the 'eggs in one basket' metaphor—different 'baskets' (phenotypes) reduce the correlation between the expected fitness of individuals.

A_{div}, the diversifying genotype posited in Table 1, is a genotype that within any generation gives rise to both dry-year and wet-year specialists. Individuals of this genotype

can be considered to 'flip' a (biased) coin to determine which phenotype they develop into (Cooper & Kaplan, 1982; Kaplan & Cooper, 1984; Seger & Brockmann, 1987). In the example, drawn from Seger & Brockmann (1987), the A_{div} genotype gives rise to dry-year specialist individuals with a probability 0.44, and the arithmetic and geometric mean fitness of this genotype were calculated using $P(\text{dry year}) = P(\text{wet year}) = ½$.

$$\mu_{div} = P(\text{dry year}) \times (0.44 \times 1 + 0.56 \times 0.6) + P(\text{wet year}) \times (0.44 \times 0.58 + 0.56 \times 1) = 0.7956, \quad (19)$$

$$G_{div} = (0.44 \times 1 + 0.56 \times 0.6)^{P(\text{dry year})} \times (0.44 \times 1 + 0.56 \times 0.6)^{P(\text{wet year})} = 0.7954. \quad (20)$$

To exemplify our use of individual-level variance and correlation, we will generalize this diversified strategy with a parameter d scaling the probability of an individual of this genotype developing into a dry-year specialist. In Fig. 4A, values $d = 0.44$ (and consequently $1-d = 0.56$) correspond to the above calculations and show the arithmetic (full line) and geometric mean (dashed line) genotypic fitness of this generalized diversified strategy. Inspecting the same graphs at $d = 0$ and $d = 1$ gives these values for the wet- and dry-year specialists A_{wet} and A_{dry}, respectively. Fig. 4B shows the individual-level variance for different degrees of diversification, and Fig. 4C shows the between-individual correlation. The geometric mean can both be calculated directly (as above) or approximated (see Section II.1*e*) by:

$$G_{div} \approx \mu_{div} - \frac{\rho_{div}\sigma^2_{div}}{2\mu_{div}}. \quad (21)$$

Here the variance (σ^2_{div}) indicates the variance at the level of an individual. This variance is calculated directly from the fitness values and their probability of occuring. Letting p_D and p_W represent the probabilities of a dry and a wet year, respectively, and $W_{DYS|D}$ be the individual absolute fitness for a dry-year specialist in a dry year (and similarly for wet-year specialists (WYS) and wet years (W). The variance is

$$\sigma^2_{div} = p_D(d \times (W_{DYS|D} - \mu_{div})^2 + (1-d) \times (W_{WYS|D} - \mu_{div})^2) + p_W(d \times (W_{DYS|W} - \mu_{div})^2 + (1-d) \times (W_{WYS|W} - \mu_{div})^2). \quad (22)$$

The correlation is defined as the covariance divided by the variance. Covariance can be expressed as $Cov(x,y) = \mathbb{E}(xy) - \mathbb{E}(x)\mathbb{E}(y)$, which gives the correlation

$$\rho_{div} = \frac{1}{\sigma^2_{div}}[(p_D(d^2 W^2_{DYS|D} + 2d(1-d)W_{DYS|D}W_{WYS|D} + (1-d)^2 W^2_{WYS|D}) + p_W(d^2 W^2_{DYS|W} + 2d\,(1-d)W_{DYS|W}\,W_{WYS|W} + (1-d)^2 W^2_{WYS|W}) - \mu^2_{div}]. \quad (23)$$

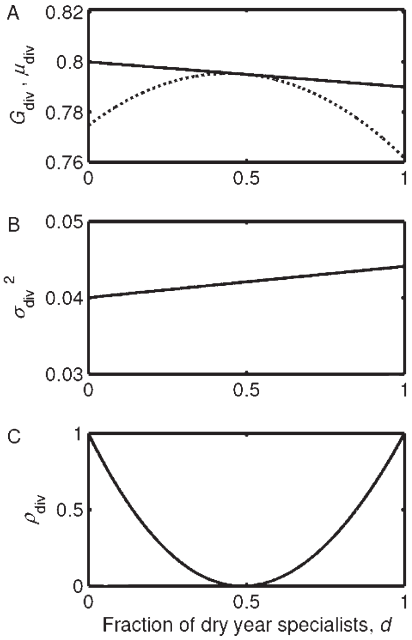

Fig. 4. The diversified allele A_{div} generalized. d scales the proportion of individuals which develop into the dry-year-specialist phenotype. (A) Arithmetic (μ_{div}, full line) and geometric mean fitness (G_{div}, dashed line). (B) The variance in fitness at the level of the individual (σ^2_{div}). (C) The correlation among individuals (ρ_{div}). The corresponding values can also be found for allele A_{dry} (at $d = 1$), and A_{wet} ($d = 0$). An allele with a diversified d such that the probability of developing into a dry-year-specialist phenotype $d = 0.44$, is the optimal one in this setting. The environment is considered coarse-grained, i.e. only temporal variability exists in the fitnesses of the phenotypes.

As is seen from this example, the diversified bet-hedging genotype achieved higher geometric mean fitness by reducing the correlation between the individuals of that genotype. If it invades a wet-year specialist ($d = 0$), this is achieved despite actually increasing the individual-level variance.

III. FROM EQUATIONS TO CONCLUSIONS: WHAT CAN WE SAY ABOUT THE DIFFERENT CATEGORIES OF BET-HEDGING?

(1) Conservative versus diversifying—endpoints of a continuum

Traditionally, bet-hedging strategies have been divided into conservative and diversified strategies (Seger & Brockmann, 1987; Philippi & Seger, 1989; Hopper, 1999; Hopper *et al.*, 2003; Rees, Metcalf & Childs, 2010). We have (Equations 7, 8) expressed the genotypic variance in fitness as a product of the individual-level variance in expected reproductive success and the correlation among individuals of the same genotype. This helps to (re-)define the different types of bet-hedging. A conservative bet-hedging genotype overcomes the cost of having a lower arithmetic mean fitness by reducing the variance in fitness σ^2_i that each individual can expect

(Equations 10, 17). Diversifying bet-hedging achieves the same by reducing the correlations (ρ_i) between the expected fitness achieved by different individuals.

Ecology and evolution are fraught with false dichotomies (for some examples, see Peters, 1991), and we believe that treating the different categories of bet-hedging as mutually exclusive would lead to this very trap. Given similar arithmetic mean fitnesses, a reduced variance at the level of the genotype is favoured regardless of whether this comes about through a reduction of expected fitness for each individual of this genotype, a reduction in the correlations among individuals, or a combination of both. In our rainfall example, the diversified bet-hedging allele A_{div} achieves a higher geometric mean fitness by a reduction in both correlation and individual-level variance if invading a population of dry-year specialists (Fig. 4, compare middle panel at $d = 1$ and $d < 1$). Thus, while at the extremes one can usefully speak of two different kinds of bet-hedging, there are all possible mixtures as well. This is often overlooked (e.g. Rees *et al.*, 2010).

(2) Between- versus within-generation bet-hedging

Bet-hedging strategies are also often categorized into between- and within-generation strategies (Hopper, 1999; Hopper *et al.*, 2003), often differentiated by the 'grain' of the environment (Levins, 1968; Hopper, 1999). In a very coarse-grained environment all individuals experience one type of environment, but over longer time scales the descendants may live in a different type of environment; this is often interpreted as the environment varying temporally. In a very fine-grained environment, individuals may experience all possible variations of the environment at the same time, thus assuming sufficient dispersal, this type of environmental variation is often equated with spatial variation (Levins, 1968; Seger & Brockmann, 1987).

In our exposition of the rainfall model, we assumed that the environment is coarse-grained: all individuals experienced either dry or wet conditions in any given year. This made the 'eggs in one basket' argument strong, since a lineage cannot survive if all its descendants perform very poorly in some years. At a different extreme, we could imagine a fine-grained environment where rainfall is very patchy such that individuals of the same generation differ in the conditions they experience. Since, as explained above, this is easier to achieve with spatial than temporal variation, the fine-grained environment is also often associated with within-generation bet-hedging, and coarse-grained environments correspondingly with between-generation bet-hedging.

All else being equal, coarser grain selects for bet-hedging far more strongly than a fine grain. A fine grain, i.e. spatial variability that occurs at a sufficiently fine scale such that offspring disperse to a diversity of habitats, would not affect the expected fitness or the variance at the individual level (σ_i^2), but it strongly reduces the fitness correlations between individuals, since in any given year individuals of the same genotype would not experience the same environment. For any given dispersal regime, then, it is hard for an individual to gain any further advantage by bet-hedging because the between-individual correlations (ρ_i) within a genotype (Equations 7–10) is already reduced to its minimum, $1/(q_i\mathcal{N})$, assuming that the fraction of dry and wet (micro-) environments within a year stays constant across years (see Appendix 1). Note that if $\mathcal{N}$ is very large, the correlations approach 0. This correlation ($\rho_i = 1/q_i\mathcal{N}$ also removes the implicit frequency dependence, because it is inversely dependent on the number of individuals of a particular genotype (q_i).

The above reasoning is the main reason why within-generation bet-hedging has been portrayed as unlikely (Hopper *et al.*, 2003). It is often thought to be an insufficient explanation for the appearance of diversified strategies. Such strategies evolve by virtue of reducing the correlation between individuals, but in large panmictic populations this correlation is already minimal because individuals of the same genetic lineage experience different environments in the same year. There is little room for any further reduction of genotypic variance (Hopper, 1999; Hopper *et al.*, 2003). This holds for fine-grained environments (Gillespie, 1974*a*, 1975), i.e. when there is no variability over time, but as soon as there is some temporal variation there is scope for a coarser grain and thus more potential for bet-hedging.

Of course, if there are no costs (i.e. the arithmetic means are the same), reduction in genotypic variance is always favoured. This can make it tempting to argue in favour of bet-hedging even if the environment is fine-grained—the variance in reproductive success will be smaller than when the grain is coarse, but there may still be room for improvement (i.e. reduction) with little cost. However, when differences in variances are minimal, bet-hedging is very easily trumped by any magnitude of costs, i.e. changes in the arithmetic mean.

It is, however, important to realize what a fine-grained environment entails in this perspective. In essence, each individual experiences either a dry or wet environment, but they all compete globally for representation in the next generation. If, on the other hand, one assumed competition to occur within each patch (for example within the patches in Fig. 5), the calculations would change (see Frank & Slatkin, 1990). For instance, such a Levene-type model can potentially give rise to coexistence, such that two alleles can coexist indefinitely and one would not necessarily go to fixation (Gillespie, 1974*b*; Levene, 1953; Frank & Slatkin, 1990). This sort of dynamics would occur if dispersal of individuals among these patches happened after local competition, such that each patch contributes an equal number of individuals to the whole population, regardless of the quality of the local environment.

An interesting thought is that dispersal itself can be viewed as a diversified bet-hedging strategy if dispersal is costly but helps to reduce the correlation of success of individuals of a lineage. The above reasoning why traits that reduce the correlation in fitness among individuals do not have much room to operate is valid if we assume that dispersal has already reduced environmental grain to a fine level (i.e. organisms spread themselves over all available habitat types in each generation). But dispersal itself is a trait that

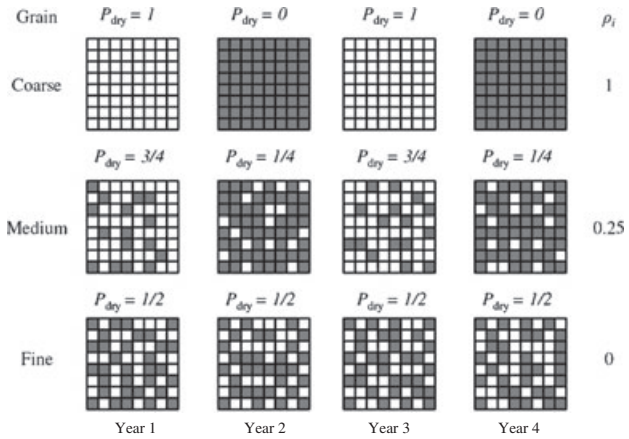

Fig. 5. Grain of the environment. Coarse-grained environments are recognized by only temporal variability; within a year all microenvironments or conditions experienced are either dry (white) or wet (grey). For fine-grained environments there is no temporal variability, and environments are steady in their composition over time ($P_{dry} = ½$, for all years). Medium-grain environments are characterized by a mixture, with both spatial and temporal variability (middle row). The ρ_i values to the right are the correlations for the genotypes A_{dry} and A_{wet} depending on the grain for infinite population sizes. In finite populations the correlation in the fine grain is $\rho_i = 1/q_iN$, where q_i is the frequency of the genotype and N is the population size, removing the 'implicit' frequency dependence in Equation 10.

can adaptively reduce this correlation—which happens if dispersal is not initially distributing individuals sufficiently across space before competition. Organisms then evolve to disperse more, partially because this reduces the correlation between individual reproductive successes. Since this may also reduce the mean success (dispersal is often costly), the definition of bet-hedging is satisfied. After this evolutionary change, the organism now experiences the scale of the grain differently. Effectively, environments become finer scaled as organisms evolve to distribute themselves across available habitats, and intriguingly this could mean that the scope for other bet-hedging strategies becomes smaller. In other words, lineages disperse to achieve a long-term fitness closer to the arithmetic mean (Kisdi, 2002) through reducing the between-individual correlation. Obviously, dispersal is not solely determined through a bet-hedging effect (kin interactions and density dependence also play a huge role, e.g. Hamilton & May, 1977; Clobert *et al.*, 2001; Ronce, 2007), but bet-hedging is clearly relevant to all arguments of dispersal that make use of the fact that a population's persistence becomes compromised if its individuals never leave the local patch. It also follows that if the effects of dispersal distance on individual variance are sex-specific, a sex bias in dispersal may evolve (Guillaume & Perrin, 2009).

(3) Between- and within-generation bet-hedging—not mutually exclusive either

In our model between-generation bet-hedging evolves more easily than within-generation bet-hedging, because a coarse grain creates more scope for selection against variance. The correlation between individuals can in many coarse-grained cases be much larger than $1/q_iN$ It is interesting that the language of 'within' *versus* 'between' generation bet-hedging suggests two distinct processes, while thinking about the grain of the environment makes it much clearer that environments do not have to be fully coarse-grained or fine-grained. For example, in our rainfall example the environment might consist of a mixture of dry and wet (micro-)environments within any given year, and the proportion of these might vary over time (see Fig. 5). In such a case, any strategy that invades due to a reduction in genotypic variance in fitness (and reduced mean fitness) can be considered a bet-hedging strategy that combines features of within- and between-generation bet-hedging.

This point can be reiterated with an example. Consider a system in which the environment varies temporally and spatially between wet and dry (i.e. medium-grained environment). We posit two kinds of years, predominantly wet or predominantly dry, such that the fractions of dry environments within a year are ¼ and ¾, respectively (as in Fig. 5, middle row). These years occur with equal frequency and no temporal autocorrelation. In such a setting, even in infinitely large populations, the correlation among individuals exceeds 0 for all strategies except the diversified strategy A_{div} with $d = 0.49$ (see Fig. 6). The correlations for alleles A_{wet} and A_{dry} can again be read off at $d = 0$ and $d = 1$, respectively: these correlations both equal ¼. That the grain of the environment is 'finer' than in our initial example can also be seen in the fact that the geometric mean fitness is now closer to the arithmetic fitness (compare Figs 4 and 6, note the change in scale on the y-axis).

The optimal strategy in this setting ($d = 0.298$) combines features of within- and between-generation bet-hedging. All individuals do not experience the same environment within a year, but the correlations between individual fitness values are also larger than 0. Also note that even though the correlation among individuals of this optimal diversified strategy is lower than for the specialists ($d = 1$ or $d = 0$), it does not reach its minimum; the genotypic variance is the product of the correlation and the variance, and the trade-off between the mean, variance and correlation need not minimize (or maximize) any of them.

IV. DISCUSSION

Bet-hedging is often expressed as a trade-off between the mean and variance that a strategy achieves (e.g. Proulx, 2000; Childs *et al.*, 2010). However, here we have shown that the trade-off is not two-way but has a triple nature. Bet-hedging can be a successful strategy despite a reduction in arithmetic mean fitness if it reduces either the individual-level variance in fitness or the fitness correlations between individuals of the same genetic lineage—or both simultaneously. This viewpoint also makes the boundaries between different

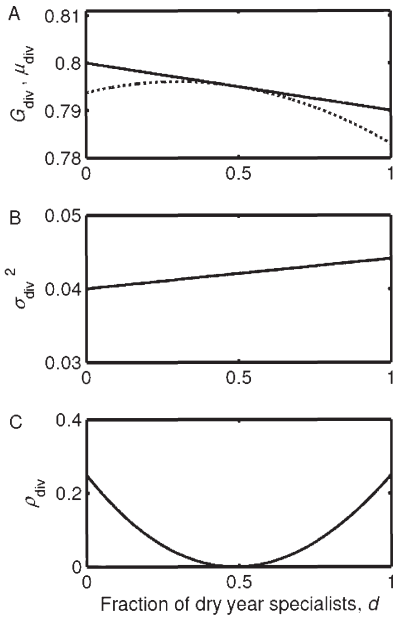

Fig. 6. The diversified allele A_{div} generalized in a medium-grained environment. A system where there are two kinds of years: predominantly dry ($P_{dry} = 3/4$) or wet ($P_{dry} = 1/4$) as in middle row of Fig. 5. The years happen in equal frequencies without autocorrelation. (A) Geometric G and arithmetic μ mean fitness of a strategy that produces d fraction of individuals with the dry-year specialist morph. (B) Individual-level variance in fitness (σ^2). (C) Correlation among individuals (ρ) of the genotype. Though any year has a mixture of both dry and wet patches, a diversified strategy has a higher geometric mean fitness than the two specialist alleles (A_{dry}, at $dV = 1$, and A_{wet} at $d = 0$). Note the different scales in A and C compared to Fig. 4.

types of bet-hedging more fluid. Traditionally, bet-hedging strategies have been divided into conservative and diversifying (sometimes with explicit statements that one of these is much more likely than the other, e.g. Einum & Fleming, 2004), whereas our analysis shows that a bet-hedger's benefit can arise through a combination of both. In our rainfall example, the allele A_{div}that creates dry- and wet-adapted individuals in each generation achieves a higher geometric mean than the dry-year specialist through a reduction in the correlation in fitness between individuals with this allele and a reduction in the individual-level variance in reproductive success, thus it is effectively a mixture of conservative and diversifying bet-hedging strategists.

Bet-hedging strategies are also often categorized into within-generation and between-generation strategies, but here, too, our analyses show that these are more appropriately seen as two ends of a continuum. Between-generation bet-hedging can occur in coarse-grain environments, where the environmental conditions vary only temporally, and within generations in fine-grained environments where spatial variation is important. Many environments are medium-grained, exhibiting a combination of temporal and spatial variability.

Throughout, we have made use of a very simple model of dry and wet years to illustrate the properties of these strategies. The insights gained can nevertheless also be used better to understand previous models invoking bet-hedging explanations, and in many cases, we believe that an explicitly combined look at both types of benefits yields more insight than a focus on one benefit only. For example, in an analysis of germination strategies and dormancy, Cohen (1966) examined the evolution of strategies that spread the germination of seeds over several years. In the light of our perspective, the optimality of this type of bet-hedging arises through a reduction in the correlation among the individual seeds of a particular lineage. This model assumes a coarse-grained environment where seeds would all have the same fitness if they all germinated within the same year. Recent analyses of systems with bet-hedging as an explanation of germination strategies (e.g. Simons, 2009) include variation in fitness across as well as within years. This provides a more complete look at the question: it makes the environment of this system medium-grained, and intriguingly this possibly reduces the need for bet-hedging arguments, since correlations among individuals germinating the same year will not be 1 as they were in Cohen's model.

We suggest that there is much scope for interpreting the numerous real-life examples of bet-hedging such that the relative roles of reduced individual-level variance and between-individual correlations are explicitly investigated. The scale of dispersal is of paramount importance here, since between-individual correlations are expected to be low to begin with if dispersal is already efficiently "hedging the bets" of genotype success in each generation by spreading individuals to different environments. The corollary is that there can be an intriguing trade-off between evolving a higher dispersal rate or longer dispersal distance and any other bet-hedging trait; an organism that hedges bets successfully with one method will not 'need' to bet-hedge as much with another (see for instance Venable & Lawlor, 1980; Snyder, 2006; Siewert & Tielborger, 2010). Crean & Marshall (2009) suggest that bet-hedging in the form of a maternal effect that diversifies offspring size should occur in a range of organisms, possibly in combination with making dispersal capacity unequal among the offspring (another type of bet-hedging). Their review points to a sea slug (*Alderia modesta*) study where mothers that produce dispersive offspring that feed exhibit higher levels of within-clutch variation in offspring size than mothers of the same species that produce far less dispersive, non-feeding offspring (Krug, 1998); such within-species variation is unexpected based on our simplistic prediction above, highlighting the need for further work.

As another example of bet-hedging, multiple mating has been proposed as a behaviour that is beneficial through individual females 'diversifying' their eggs over several males (Fox & Rauter, 2003; Forsman, Ahnesjo & Caesar, 2007), avoiding the risk of mating with a low-quality male. In the model presented here, the environment can be considered fine-grained if the quality of males is constant across years and competition among offspring is global. In such an environment the correlation among these mating females is already at its minimum, and if there is only a slight cost

of mating multiply, multiple mating is only favoured by bet-hedging mechanisms for small population sizes (Yasui, 2001).

Ideas of bet-hedging are often invoked for any behaviour that is 'diversified', but it is important to realize that bet-hedging is defined through its three effects listed above (reduced arithmetic mean together with a reduced variance and/or between-individual correlation in fitness), and there are many instances of 'diversification' that bring about a benefit *via* other mechanisms than actual bet-hedging. Multiple mating, for example, can also be selected for to increase the genetic diversity within a clutch to reduce kin competition among the individual offspring (Forsman *et al.*, 2007), and obviously there are many explanations of multiple mating that are solely based on increasing numbers of offspring for either males or females (Arnqvist & Nilsson, 2000; Jennions & Petrie, 2000; Panova *et al.*, 2010). The evolutionary benefit of 'spreading' offspring across time and space could similarly be based on the direct effect of reduced kin competition in contexts such as dormancy and dispersal (Hamilton & May, 1977; Venable & Lawlor, 1980; Ellner, 1986). In many cases such diversification will also reduce the correlation among individuals, yet it need not be a bet-hedging strategy. Strictly speaking, a bet-hedging strategy requires a reduction in the arithmetic mean coupled with a reduction in individual level variance, correlation among individuals, or both.

V. CONCLUSIONS

(1) Bet-hedging strategies increase their own probability of fixation through a reduction in genotypic mean fitness accompanied by a reduced genotypic variance in fitness.

(2) Reduction in genotypic fitness variance can be accomplished through a reduction in the variance of fitness at the level of the individual, a reduction in the correlation of fitness between individuals of a genotype or a combination of both. This also implies that reduction in genotypic fitness can be achieved despite an increase in individual-level variance (or correlation) as long as correlations (or individual-level variance) are similarly decreased.

(3) Conservative bet-hedging strategies are recognized by a reduction in individual-level variance in fitness.

(4) Diversified bet-hedging strategies are recognized by a reduction in between-individual correlations in fitness.

(5) Since individual-level variance and between-individual correlations can be changed independently, conservative and diversified bet-hedging strategies is a false dichotomy; they are better viewed as two extremes. Possible bet-hedging strategies can incorporate any combination of individual-level variance and correlation that reduces genotypic variance in fitness. It is also important to keep in mind that a comparison of strategies can lead to one being superior in having both a higher mean and lower fitness variance; there is then no trade-off between these components predicting evolutionary success.

(6) Between-individual correlations depend on the grain of the environment; within-generation bet-hedging can occur under a fine-grained environment, effectively reducing the correlation in fitness between individuals to its minimum (inversely proportional to the population size).

(7) Within-generation and between-generation bet-hedging is also a false dichotomy; bet-hedging strategies can occur under any grain of the environment effectively being a combination of between-generation and within-generation characteristics.

VI. ACKNOWLEDGEMENTS

Barbara Fischer sweetened the mathematical exposition and FaKuTsI gave access to knowledge.

VII. APPENDIX 1. DERIVATION OF THE GENERAL MODEL

We posit a population of size N with two alleles at a haploid locus (with frequencies q_1 and q_2) and denote the genotypic mean absolute fitnesses (or mean reproductive successes) as

$$R_1 = \frac{1}{Nq_1}\sum_{j=1}^{Nq_1} \mu_1 + \alpha_{1,j} = \mu_1 + \bar{\alpha}_1, \tag{A1}$$

$$R_2 = \frac{1}{Nq_2}\sum_{j=1}^{Nq_2} \mu_2 + \alpha_{2,j} = \mu_2 + \bar{\alpha}_2. \tag{A2}$$

Where μ_i represents the arithmetic mean absolute fitness of an individual of the ith genotype, and $\alpha_{i,j}$denotes the deviation from this expectation for the jth individual of the ith genotype. For a given year $\bar{\alpha}_i$denotes mean deviation for the genotype. We also have

$$\bar{R} = q_1 R_1 + q_2 R_2 \tag{A3}$$

which is the mean absolute fitness in the population. The frequency of the first genotype in the next generation will be

$$q'_1 = q_1 \frac{R_1}{\bar{R}}. \tag{A4}$$

This is where trouble arises in the view of fitness as a random variable, because a ratio of random variables is difficult to deal with. We continue by stating that the expected change in the frequency of the first allele will be

$$\mathbb{E}[\Delta q_1] = \mathbb{E}[q'_1] - q_1 = \mathbb{E}\left[\frac{q_1 R_1}{\bar{R}}\right] - q_1 \tag{A5}$$

where $\mathbb{E}$ is taken to mean expectation. We rearrange this as done in most population genetics treatments (see e.g. Rice, 2004)

$$\mathbb{E}\left[\frac{q_1 R_1}{\bar{R}}\right] - q_1 = \mathbb{E}\left[\frac{q_1 R_1}{\bar{R}}\right] - \frac{q_1 \mathbb{E}[\bar{R}]}{\mathbb{E}[\bar{R}]}$$

$$= \mathbb{E}\left[\frac{q_1 R_1 - q_1 \mathbb{E}[\bar{R}]}{\bar{R}}\right] = \mathbb{E}\left[\frac{q_1 R_1 - q_1(q_1 R_1 + q_2 R_2)}{\bar{R}}\right]$$

$$= \mathbb{E}\left[\frac{q_1(R_1(1-q_1)-q_2R_2)}{\bar{R}}\right] = \mathbb{E}\left[\frac{q_1(R_1q_2-q_2R_2)}{\bar{R}}\right]$$
$$= \mathbb{E}\left[\frac{q_1q_2(R_1-R_2)}{\bar{R}}\right] \quad \text{(A6)}$$

On this last expression we will use the delta-method (e.g. Lynch & Walsh, 1998; Rice & Papadopoulos, 2009) to expand this in a series. An expression for the expectation of a ratio of two random variables a and b is given by

$$\mathbb{E}\left[\frac{a}{b}\right] = \frac{\mathbb{E}[a]}{\mathbb{E}[b]} + \sum_{k=1}^{\infty}(-1)^k \frac{\mathbb{E}[a] \ll {}^k b \gg + \ll a, {}^k b \gg}{\mathbb{E}[b]^{k+1}}. \quad \text{(A7)}$$

Here $\ll \ \gg$ denotes higher moments. For instance $\ll {}^k b \gg$ is the kth central moment of the random variable b, which for $k = 1$ is zero, for $k = 2$ is the variance. Mixed moments are defined as

$$\ll a, {}^k b \gg = \mathbb{E}\{[a - \mathbb{E}(a)][b - \mathbb{E}(b)]^k\} \quad \text{(A8)}$$

which for $k = 1$ is the covariance between a and b.

We can here put in R_1 for a and $\bar{R}$ for b. Then using the expansion A7 on A6 we get

$$\mathbb{E}\left[\frac{q_1q_2(R_1-R_2)}{q_1R_1+q_2R_2}\right] = \frac{\mathbb{E}[q_1q_2(R_1-R_2)]}{\mathbb{E}[q_1R_1+q_2R_2]} + \sum_{k=1}^{\infty}(-1)^k \frac{\begin{array}{r}\mathbb{E}[q_1q_2(R_1-R_2)] \ll {}^k\overline{R} \gg \\ + \ll q_1q_2(R_1-R_2), {}^k\overline{R} \gg\end{array}}{\mathbb{E}[\bar{R}]^{k+1}} \quad \text{(A9)}$$

The 1st central moment of $\bar{R}$ is 0 (so the first part in the numerator is 0 for $k = 1$), and assuming the higher orders are negligible, we are only interested in the first part of this sum, we need the 1st mixed moment, i.e.

$$\ll q_1q_2(R_1-R_2), {}^1\overline{R} \gg = Cov(q_1q_2(R_1-R_2), \overline{R}). \quad \text{(A10)}$$

One nice rule about covariances of a sum of random variables is

$$Cov(aX+bY, cW+dV) = acCov(X,W) + adCov(X,V) + bcCov(Y,W) + bdCov(Y,V), \quad \text{(A11)}$$

we want:

$$Cov(q_1q_2R_1 - q_1q_2R_2, q_1R_1 + q_2R_2). \quad \text{(A12)}$$

Substituting $a = q_1q_2, b = -q_1q_2, c = q_1, d = q_2$ and $= W = R_1, Y = V = R_2$ in A11 this covariance becomes:

$$Cov(q_1q_2R_1 - q_1q_2R_2, q_1R_1 + q_2R_2) = q_1^2q_2Cov(R_1,R_1) + q_1q_2^2Cov(R_1,R_2) - q_1^2q_2Cov(R_2,R_1) - q_1q_2^2Cov(R_2,R_2) \quad \text{(A13)}$$

and, since $Cov(x,x) = Var(x)$ and $Cov(x,y) = Cov(y,x)$, this is:

$$Cov(q_1q_2R_1 - q_1q_2R_2, q_1R_1 + q_2R_2) = q_1q_2(q_1Var(R_1) - q_2Var(R_2) + (q_2-q_1)Cov(R_1,R_2)) \quad \text{(A14)}$$

Thus keeping only the first two terms in the expansion above we get:

$$\mathbb{E}\left[\frac{q_1q_2(R_1-R_2)}{q_1R_1+q_2R_2}\right] \approx \frac{\mathbb{E}+[q_1q_2(R_1-R_2)]}{\mathbb{E}[q_1R_1+q_2R_2]} + \frac{q_1q_2(q_2Var(R_2) - q_1Var(R_1) + (q_1-q_2)Cov(R_1,R_2))}{\mathbb{E}[q_1R_1+q_2R_2]^2} \quad \text{(A15)}$$

Note the change of $-$ into $+$ before the last fraction and inside it.

Assuming that $\bar{\mu} = q_1\mu_1 + q_2\mu_2 \approx 1,$, the denominators are both 1. In addition, since the allele frequences are not random variables they can be taken out of the expectations and we get:

$$\mathbb{E}\left[\frac{q_1q_2(R_1-R_2)}{q_1R_1+q_2R_2}\right] \approx q_1q_2\{(\mu_1-\mu_2) + [q_2Var(R_2) - q_1Var(R_1) + (q_1-q_2)Cov(R_1)]\} \quad \text{(A16)}$$

This is identical to Frank & Slatkin's (1990) Equation 7.

We go on to note that we started with introducing individual deviances from the mean reproductive success of a genotype ($\alpha_{i,j}$) and that the genotypic variances and covariance can be written as:

$$Var(R_i) = \rho_i\sigma_i^2; \quad \text{(A17)}$$
$$Cov(R_1,R_2) = \rho_{12}\sigma_1\sigma_2. \quad \text{(A18)}$$

These variances are the way Frank & Slatkin (1990) originally presented them, but they deserve some elaboration. Strictly speaking, the relation between the variance of a mean of n random variables with equal variance and the variances of the individual random variables is

$$Var(\bar{X}) = \frac{\sigma^2}{n} + \frac{n-1}{n}\bar{\rho}\sigma^2 = \sigma^2\left(\frac{1}{n} + \frac{n-1}{n}\bar{\rho}\right) \quad \text{(A19)}$$

where σ^2 is the variance of the individual random variables and $\bar{\rho}$ is the average correlation between the variables. Stricly speaking, we (in A17) use the correlation as

$$\rho_i = \left(\frac{1}{Nq_i} + \frac{Nq_i-1}{Nq_i}\bar{\rho}\right). \quad \text{(A20)}$$

This means that for a given genotype the minimum value possible for this between-individual correlation is $1/Nq_i$, which is the case if all individuals of the ith genotype have mean ($\bar{\rho}$) correlation of 0 (which this mean can not be lower than). For large population sizes, these measures are

practically identical. Note, however, that the correlation across genotypes can take any value between 1 and −1.

Above we assumed that the higher orders of the series expansion was negligible, by keeping only the first term of the infinite series in Equation A9. Technically speaking, this is not always justifiable, since the series need not converge quickly enough. For examples of when these higher orders become important for predicting allele changes, see Rice (2008) and Rice & Papadopoulos (2009).

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