Trans-generational plasticity and bet-hedging: a common eco-evolutionary framework of utter relevance for climate change adaptation.

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Abstract

Organisms are typically assumed to respond to environmental change by genetic adaptation, phenotypic plasticity, or by genetic adaptation *of* phenotypic plasticity - the latter is in the focus of contemporary calls for an extended evolutionary synthesis, because it impacts evolutionary dynamics by tinkering with the raw material for selection (phenotypes). Diversified bet-hedging, a risk-spreading strategy that affects the phenotypic variance among one's offspring, can provoke a similar impact, yet it is rarely considered in studies of climate change adaptation. We argue that this is due to plasticity being overly synonymized with phenotypic variance and GxE interactions, and thus strive for a unifying framework: we clarify that diversified bet-hedging and plasticity are mutually exclusive strategies, arising from opposing changes in reaction norms (allocating phenotypic variance among or within environments). Since these two strategies have in common that they shape phenotypic variance within populations, both may determine evolutionary dynamics and hence resilience to climate change. We advocate that a paradigm shift is required to accommodate the role of bet-hedging in evolution.

Key words: Phenotypic plasticity, Bet-hedging, GxE, Canalization, Adaptation, Climate change

Climate change: coping with variance

Environments are heterogeneous, and organisms cope with this variation in multiple ecological and evolutionary ways. The optimal strategy to deal with environmental variation in time and space will largely depend on the extent of its predictability along these two dimensions (Southwood 1977). Obviously, unpredictable short-term temporal fluctuations have different effects than predictable changes that occur over the course of an individual's life time, or those proceeding gradually over multiple generations.

Global CO_2 concentrations are acceleratingly rising since at least 100 years (IPCC 2014). The lack of long-term predictability puts species at risk (Urban 2015), thus global biodiversity will likely decrease within this century (Midgley et al. 2002; Visconti et al. 2016; Tilman et al. 2017), thereby likely provoking a sixth mass-extinction (Barnosky et al. 2011). Changes in short-term climate variability (IPCC 2014; Bathiany et al. 2018) and its temporal autocorrelation (Lenton et al. 2017) impose further challenges, such as affecting food web stability (Yang et al. 2019) and separating ectotherm preferences from their thermal optima (Kingsolver and Buckley 2017). The twofold challenge of changing means and changing variability is one of the most urgent societal problems.

In view of recent climatic change the role of phenotypic plasticity has been aptly discussed: multiple timely reviews have highlighted the importance of phenotypic plasticity not only in coping with changing environments, but also in steering the evolvability of traits in a changing climate (Fox et al. 2019). Diversified bet-hedging, i.e. adaptive variance in offspring phenotypes, on the other hand is surprisingly rarely associated with climate change and with trait evolvability. The lack of clarity in the definition of both bet-hedging and phenotypic plasticity did neither promote an integrated view: plasticity refers typically to reaction norm shapes and their evolutionary outcome, while bet-hedging is defined only as an evolutionary risk spreading strategy. We here unify the two strategies in a common eco-evolutionary framework. We first provide a short review of the mechanisms underlying plasticity and bet-hedging, subsequently provide a common framework for their analysis and interpretation and end with outstanding question in terms of understanding and predicting species' adaptation to climate change.

Plasticity: adapting to changing environments

Phenotypic plasticity, the ability to match the phenotype with the environment, is a cornerstone of ecological and evolutionary theory (West-Eberhard 2003; Pigliucci 2005; Laland et al. 2015). Our modern view of plasticity (Bradshaw 1965) is based on the combination of phenotypic variation with Woltereck`s (1913) concept of a reaction norm (Nicoglou 2015). A reaction norm describes how a phenotype changes with the environment, and plasticity is considered the shape of such a reaction norm. This explicit focus on a reaction norm makes plasticity an ecological *process* with which organisms cope with environmental change. In contrast to the above definition, one can also regard plasticity by its *outcome* on evolution: Nongenetic variation (or environmental variance, σ_E^2) reduces the heritability of a trait, $h^2 = \frac{\sigma_G^2}{\sigma_E^2}$

(Wright 1920) and hence the response to selection via the breeder's equation, $R = h^2 * S$. Importantly, environmental variance may not only include plasticity but also an "error" term, for example developmental noise may increase non-heritable variation. Nevertheless, this detail is frequently overlooked, and plasticity is used synonymously for phenotypic variance. It is hence not a surprise that plasticity has been considered a nuisance parameter in evolutionary biology (Falconer 1952). Since the 1980s it has, however, become apparent that plasticity itself is a trait that can evolve (Via and Lande 1985; Schlichting 1986; Nicoglou 2015), and it is this focus on evolutionary outcomes that received most attention in light of recent climate change. For example, plasticity in egg laying dates of *Parus major* has increased in response to an increasing mismatch with food peak abundance, and this plasticity included a significant heritable component (Nussey et al. 2005).

The evolution of plasticity is analogous to any other trait that is molded by selection, but different as it creates novel eco-evolutionary feedbacks that may alter the course and speed of evolution (De Jong 2005; Morgan 2019). These changes are so far-reaching that there have been repeated calls for a novel evolutionary synthesis, with plasticity taking a prominent place (West-Eberhard 2003; Laland et al. 2015). Several excellent recent reviews exist (e.g. Morgan 2019), so we will only name the most important concepts here. In short, directional selection may first favour plasticity. While plastic expression of the extreme phenotypes buys time and shields the genotype from selection, the less extreme phenotypes fall out of use (genetic accommodation), and stabilizing selection may then canalise the phenotype to the new mean value (genetic assimilation). These patterns can lead to the inheritance of acquired characteristics, which puts the whole concept of heritability in question.

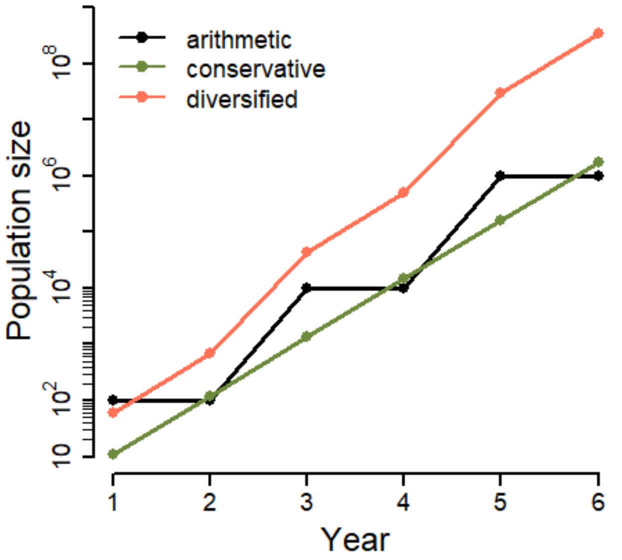
The focus on evolutionary consequences of phenotypic plasticity have changed the meaning of the term from a process to that of a – usually – adaptive strategy. Plasticity is now commonly used both for reaction norm shapes and phenotypic variance, commonly ignoring that reaction norms need not be adaptive, and that phenotypic variance need not rely on plasticity.

Bet-hedging: surviving in variable environments

Bet-hedging is generally defined by its effects on fitness - it encompasses strategies that reduce fitness variance at the cost of arithmetic mean fitness. It seems odd that such a strategy may be favored by selection, but fitness variance can have devastating consequences for fitness (see box 1 for a numerical example), e.g. when an extreme environmental condition in a single year drives a genotype to extinction. This is because long-term fitness is based on reproduction, which is a multiplicative process, and thus best described by the geometric rather than the arithmetic mean. The geometric mean is sensitive to variance, so a lower, but less fluctuating reproductive output can pay off (Cohen 1966). There are two fundamentally different ways of reducing fitness variance, namely conservative and diversified bet-hedging (Seger and Brockmann 1987; Starrfelt and Kokko 2012). The conservative bet-hedger avoids risks and, for example, advances hibernation to reduce fitness costs of early frosts. The lower fitness variance can offset the costs in mean fitness, which are caused by a reduced season length and hence lower growth rates. In contrast to conservative bet-hedgers the diversified bet-hedger does not directly avoid risks. Instead, it produces a mixture of offspring phenotypes with varying strategies, some of which do not obtain highest arithmetic mean fitness. This strategy increases fitness variance among siblings, but because fitness among siblings is not multiplicative, its variance is not detrimental. On the contrary, low fitness of some siblings is averaged out by the arithmetic mean, which in turn reduces the (geometric) fitness variance among years and hence leads to less fluctuating growth rates. Hence, both bet-hedging strategies have in common that they maximize geometric mean fitness by decreasing fitness variance, at the cost of the arithmetic mean.

Box 1: A bet-hedging example

Aphids reproduce by parthenogenesis during summer, which enables quick population growth; in winter frost kills the soft-bodied insects and only diapausing eggs survive (Simon et al. 2002). The struggle to keep the growing season long on one hand and to avoid death on the other hand puts diapause timing under intense selection pressure. In the following we will consider three strategies to cope with unpredictable conditions. First, a genotype may time diapause such that it coincides with mean winter onset (arithmetic mean optimization); this is the strategy that may be intuitively expected. This genotype profits from high offspring numbers (say, 100 offspring) in half of the years, i.e. when winter is later than in an average year, but high mortality (1 surviving offspring) in the other half. A second genotype, the conservative bet-hedger, may diapause earlier in the year and may have 11 offspring regardless of winter onset. Thirdly, a genotype may reproduce with a mixed strategy(diversified bet-hedging), in which half of the offspring follow the first strategy and the other half follow the second strategy. The arithmetic mean offspring numbers are thus 50.5 ($\frac{100+1}{2}$) for the first genotype, but only 11 for the second and 30.75 ($\frac{50.5+11}{2}$) for the third genotype. Nevertheless, the bet-hedging strategies already pay off after four years, because the high between-years variance stalls the exponential growth of genotype 1 (see figure). This shows that the arithmetic mean does not adequately describe fitness (Seger and Brockmann 1987; Simons 2011; Starrfelt and Kokko 2012).



Bet-hedging is beneficial exactly under those conditions that do not allow for plasticity, i.e. rapidly fluctuating environments. When environments are unpredictable, the evolutionary bets may be hedged in space or time (Buoro and Carlson 2014), or in identity (by facultative sexuality, Gerber and Kokko 2018). Typical examples are seed banks of desert annuals (Cohen 1966); diapausing strategies of annual killifish (Furness et al. 2015) and of insects (Hopper 1999); facultative sexuality of aphids (Halkett et al. 2004); and dispersal polyphenisms

(Grantham et al. 2016). There has been ample theoretical work on the factors that allow for the evolution of bet-hedging, such as little temporal (Scheiner 2014a), or for dispersal traits, spatial autocorrelation of the environment (Venable and Brown 1988), and high costs of phenotypic plasticity (Maxwell and Magwene 2017). On the other hand, it is less clear how prevalent bet-hedging is in nature (Simons 2011). In contrast to phenotypic plasticity, bet-hedging requires evidence for a lack of correlations with the environment, making the existence of bet-hedging strategies very difficult to prove. Due to the dearth of proven cases of bet-hedging, studies on the eco-evolutionary dynamics (e.g. population persistence, demographic consequences) are largely missing (Buoro and Carlson 2014). Hence bet-hedging is well established in theory, but its relevance is not known.

Bet-hedging and plasticity: complementary or related?

Bet-hedging theory assumes that environmental conditions are entirely unpredictable, which is obviously not the dominantly prevailing case in nature. In reality genotypes should maximise the use of information by adjusting their phenotype to the environmental context, unless phenotypic plasticity carries high costs (Donaldson-Matasci et al. 2013). In other words, bet-hedging and plastic strategies do not stand on their own, but should be jointly integrated in individual strategies. Theoretical models often account for this complementarity, and define bet-hedging as either variance of reaction norms (Westneat et al. 2015) or as a separate developmental instability trait (Scheiner 2014b; Tufto 2015), allowing bet-hedging to evolve independently from plasticity. We argue, however, that the association of bet-hedging and plasticity runs even deeper than mere complementarity, and that plasticity and bet-hedging are, in fact, mechanistically related.

In general, there are two theories regarding the creation of adaptive phenotypic variance: First, adaptive variance in traits can be achieved by overly relying on cues with little predictive power ("microplasticity", Simons and Johnston 2006; "hyperplasticity", Scheiner and Holt 2012). For example (Maxwell and Magwene 2017) engineered a yeast model that evolved a response to estradiol, a compound that was entirely unrelated to fitness but ensured phenotypic variance in a fluctuating environment. Secondly, diversified bet-hedging strategies may be achieved by developmental instability (e.g. Simons and Johnston 1997; Veening et al. 2008). Low copy numbers e.g. of transcriptional regulators may cause sampling errors which get amplified in the protein regulatory network (Kærn et al. 2005). This results in phenotypic variance, either of single cells (Volfson et al. 2006) or among cells of the same organism (Woods 2014; Dueck et al. 2016). In the extreme case the variance affects developmental pathways and causes random determination of alternative phenotypes (Perrin 2016). We argue that this second mode of creating variance is not an alternative to, but a special case of microplasticity – the only difference is that the plastic reaction is on the cellular level rather than a reaction to the macroscopic environment. Thus, no matter how phenotypic variance is achieved, it can be described by reaction norm slopes, putting current modelling approaches into question.

There is another property of bet-hedging which requires careful consideration: it is the solution to an information theoretical problem (Donaldson-Matasci et al. 2013), and hence inherently dichotomous (Cooper and Kaplan 1982). For example, an organism may face the decision to germinate or to remain dormant (Cohen 1966), to produce sexual forms or to remain parthenogenetic (Gerber and Kokko 2018), or to allocate energy to current or to the next offspring (Marshall et al. 2008). Even if the phenotype appears to be continuous (e.g. years of dormancy; clutch size), the decision process can be decomposed into a temporal sequence of "coin-flipping" events (Cooper and Kaplan 1982). Therefore bet-hedging can be expressed by a polyphenic reaction norm. We find this relationship between plasticity and bet-hedging highly problematic, as the basic assumptions of plasticity/bet-hedging models are violated. We are not alone with this view – a recent publication noted the formal similarity of bet-hedging and plasticity (Xue and Leibler 2018) and called for a unification of the two strategies. We hence wish to clarify the definitions of plasticity and bet-hedging in environments of varying predictability.

Bet-hedging, canalization and plasticity: a problem of variance partitioning

As outlined above we find it crucial to make a distinction between ecological mechanisms and emerging strategies. We will thus first introduce a set of terms to describe reaction norm shapes and then another set of terms to describe the resulting evolutionary strategies.

Let us focus on a polyphenic reaction norm, describing for example germination. Each offspring can be in one of two states, as it can either stay dormant or germinate. The probability of each state – or, from the mother's perspective, the proportion of offspring – in response to an environmental cue can be described by a reaction norm (Fig. 1A). We assume that the shape of the reaction norm has a logistic shape, though our concepts are valid for any reaction norm that is bounded between 0 and 100%. The phenotype distribution depends in this case on range, mean and slope of the curve: first, a phenotype may exhibit a steep slope and high range, such that the phenotype changes radically in response to the environment (see upper right in Fig. 1B). This shape maximizes the variance among environments, which we will refer to as σ^2_{among}. Secondly, the reaction norm may be flat (upper left). In this case, there is no variance among environments, but within each environment phenotypes may take one of two forms in probabilistic fashion. The variance of these phenotypes within each environment (σ^2_{within}) is calculated as p * (1-p), since the trait choice is a Bernoulli draw, and hence maximized with a flat reaction norm at the 50% level. The two variance components complement each other, i.e. it is not possible to maximize both σ^2_{among} (steep slope, high range) and σ^2_{within} (minimal departure from 50%). Combinations of the two components are however possible (middle column), and the ratio of the variances is determined by the range and slope of the reaction norm. Alternatively, a reaction norm may contain neither variance component, which can be achieved by moving the elevation of the reaction norm to 0 or 100% (lower row). Such a reaction norm represents a highly canalized phenotype, thus we express the degree of canalization as the sum of the variance components. Lastly, the curve may shift on the x-axis, which influences the mean phenotype rather than phenotypic variance (Fig. 1C). Reaction norms can therefore vary along three axes: in their mean, in the variance composition (σ^2_{among} : σ^2_{within}), and in the degree of canalization (σ^2_{among} + σ^2_{within}).

From mechanisms to strategies

Starrfelt & Kokko (2012) have defined fitness optimization as a trade-off among arithmetic mean optimization, avoidance of fitness variance (conservative bet-hedging) and avoidance of fitness correlations in the offspring (diversified bet-hedging). We extend this concept by linking it with distinct changes in reaction norm shapes, and by adding phenotypic plasticity. We thus identify three axes along which organisms may optimize geometric mean fitness (Fig. 1): First, genotypes may vary in their degree of canalization, which we expressed by the sum of the variance components. We expect the level of canalization to evolve in response to environmental variability, and we call the according strategy responsiveness. To distinguish the evolutionary outcomes from their process, we reserve the term canalization for descriptions of the reaction norm, and instead refer to the extreme strategies on the responsiveness axis as "fixed" and "flexible". Secondly, the mean of the reaction norm may vary. Depending on environmental predictability, it should strike a balance among arithmetic mean optimization and conservative bet-hedging. We call this axis of adaptive strategies variance avoidance. Lastly, the variance composition (among versus within environments) should depend on environmental predictability, leading to phenotypic plasticity or diversified bet-hedging as extremes on an axis of information reliance. We thus no longer define plasticity and bet-hedging as physiological processes (reaction norm shapes), but as emerging strategies, and we will keep to this definition for the remainder of this essay.

Fitness optimization along three axes

Our definition extends classical concepts of bet-hedging. Plasticity was not seen as a bet-hedging trait (Seger and Brockmann 1987), and bet-hedging not as a plastic trait in the strict sense (Cooper and Kaplan 1982). Nevertheless, bet-hedging is sometimes regarded the product of plasticity (Simons and Johnston 2006; Maxwell and Magwene 2017). We resolve the confusion around these terms by distinguishing reaction norm shapes and emerging strategies, and show that plasticity and diversified bet-hedging mark the two extremes on a continuum of strategies. By removing the dichotomy of bet-hedging versus plasticity, we stimulate research on the joint eco-evolutionary consequences of the information reliance axis.

Another common point of confusion is the term canalization, which is sometimes seen as the opposite of plasticity (e.g. Van Kleunen and Fischer 2005; Ghalambor et al. 2007; Reed et al. 2010). To prove the point, the attentive reader will have noted that we ourselves have introduced plasticity as the only component of non-genetic variance in the heritability equation. This follows a long tradition of ignoring bet-hedging in the context of climate change, e.g. by equating Gene x Environment interactions with plasticity alone. We emphasize however, that phenotypic variance includes *all* facets of variation, including diversified bet-hedging. In discussing heritability, we therefore advocate partitioning phenotypic variation into:

$h^2 = \frac{\sigma_G^2}{\left(\sigma_{Eamong}^2 + \sigma_{Ewithin}^2 + \sigma_{error}^2\right)}$, where σ_{error}^2 refers to measurement error.

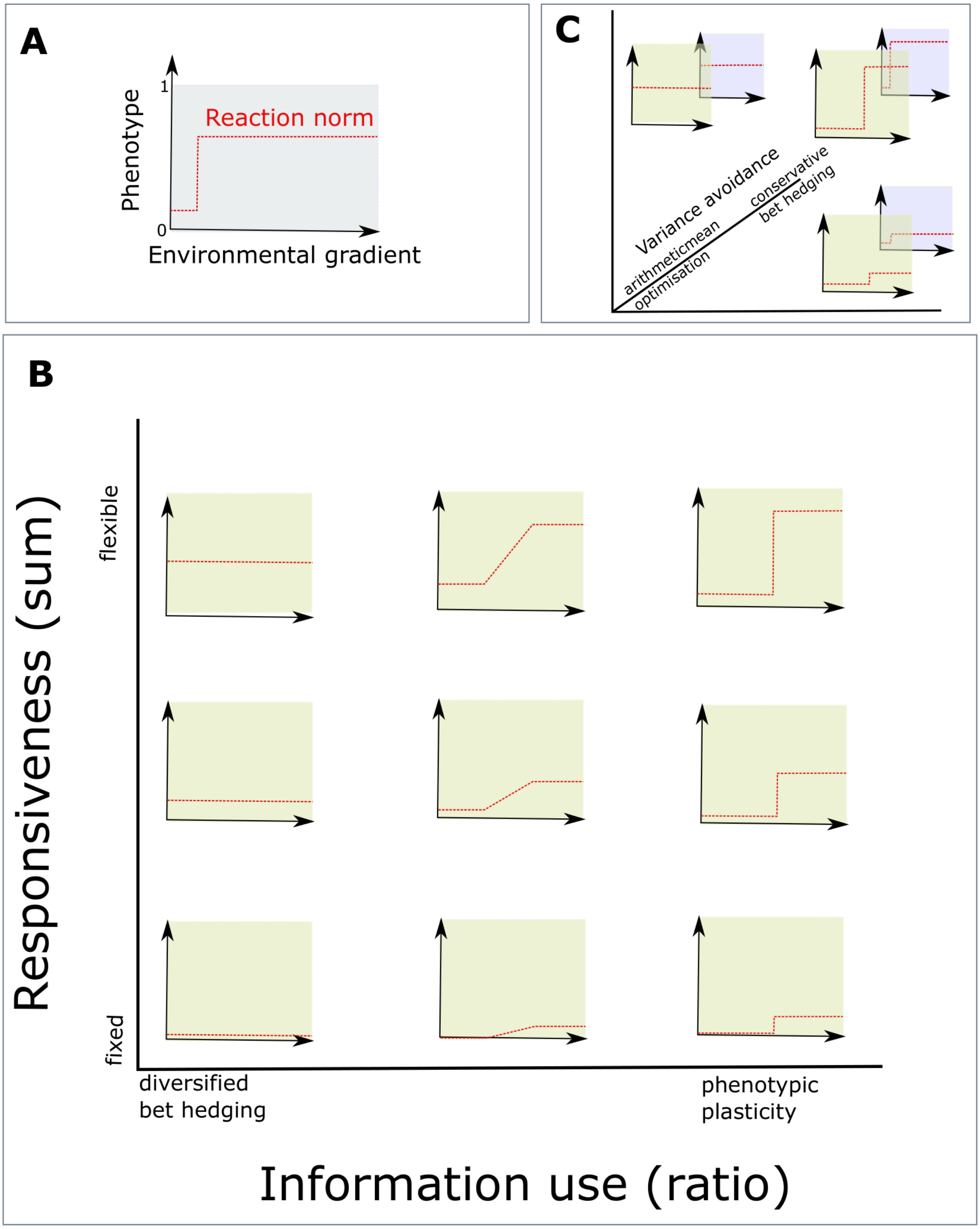


Fig. 1. Relationship of evolutionary strategies with reaction norm properties. Panel A shows a dichotomous reaction norm. The decision to switch phenotypes can be expressed by a steep logistic curve. Reaction norms can divert in various ways from this step function: By changes in the ratio (x-axis) and sum (y-axis) of the variance components σ^2_{among} and σ^2_{within}(Panel B), and by changes in the mean (Panel C). Axes describe the resulting evolutionary strategies.

Equating phenotypic variance only with plasticity is precisely what prevented bet-hedging from being acknowledged as major force in evolution. Future research needs to shed light on the evolvability, as well as potential differences in GxE covariances of each variance component.

Thirdly, we placed conservative bet-hedging and mean optimization on the same axis. This emphasized that conservative bet-hedging and diversified bet-hedging are different despite both relying on unpredictability. The two strategies have been separated early on (Seger and Brockmann 1987), yet are often discussed in conjunction (e.g. Simons 2011). In our view conservative and diversified bet-hedging should not be contrasted to each other, but discussed in conjunction with arithmetic mean change (Starrfelt and Kokko 2012) and phenotypic plasticity. Overall, our concept provides a fitness landscape along which genotypes may evolve and studying each axis by its own is not fruitful. For example, failure to shift in means with climate change is not problematic per se – it could be mitigated by concurrent changes in responsiveness. Similarly, the lack of both phenotypic plasticity and mean change may not have severe fitness consequences, if the lack of plasticity is mitigated by diversified bet-hedging. It is the combination along all three axes that defines fitness in a given environment.

Concluding remarks and future perspectives

Our framework establishes a firm distinction between transgenerational plasticity and diversified bet-hedging, and allows evaluating the eco-evolutionary consequences of all aspects of phenotypic variance. We predict that future advances will stem from research along three frontiers: by providing empirical data along a bet-hedging – plasticity continuum; with the help of theoretical models on eco-evolutionary consequences; and a careful review of traditional bet-hedging predictions.

Empirical data for bet-hedging is notoriously difficult to obtain (Simons 2011), and we are concerned that the less clear-cut case of partially predictive environments will pose further challenges. We argued that the distinction among diversified bet-hedging and plasticity lies in the shape of the reaction norm, which requires studies that go beyond the slope and consider reaction norms under more than three environmental conditions. Such high-resolution data across environments with varying predictability is obviously difficult to obtain – nevertheless there are valuable exceptions (Murren et al. 2014), and the gaining momentum of open data principles and meta-analytic techniques offers exciting novel opportunities.

We hope that our framework will also stimulate modelling approaches on the evolution along a plasticity – bet-hedging continuum. Current models usually assume independent evolution of bet-hedging and plastic strategies (e.g. Scheiner 2014b), but explicitly incorporating reaction norm change, and thus linking the two strategies, may lead to novel insights. The other direction, how the evolution of bet-hedging strategies affects ecology, is rarely studied (but see Libby and Ratcliff 2019), and we are not aware of any theory that explores the role of bet-hedging in shaping evolution. One critical step for all these models will be incorporating the multidimensionality of environmental traits to allow the evolution of bet-hedging through microplasticity to uncorrelated cues.

Box 2: Costs and limits of the bet-hedging – plasticity continuum

Bet-hedging and plasticity have, by definition, important disadvantages: bet-hedging reduces arithmetic mean fitness and plasticity may cause phenotype-environment mismatches. Although these apparent disadvantages are only the flip sides of otherwise adaptive strategies, there may be also true evolutionary constraints. Dewitt et al. (1998) provided a useful concept for plasticity, classifying its costs and limits, and suggested the following costs:

1) *Maintenance costs*: costs of having a plastic genotype;
2) *Production costs*: costs of producing a phenotype by plastic development as compared to fixed development;
3) *Information acquisition costs*: costs of acquiring information about the environment;
4) *Developmental instability costs*: costs from non-canalized, imprecise development (e.g. fluctuating asymmetry)
5) *Genetic costs*: costs imposed by epistatic interactions and pleiotropic genes.

The latter three costs were later criticized to be no distinct category (Van Kleunen and Fischer 2005; Auld et al. 2010), but rather special cases of production or maintenance costs. The limits of plasticity were separated into:

1) *Information reliability limits*: environments are rarely perfectly predictable;
2) *Lag-time limits:* plastic development requires time;
3) *Developmental range limits:* fixed development may achieve more extreme phenotypes;
4) *Epiphenotype limits:* late addition of development traits to existing body plans is less effective than canalized development.

Similar discussions on constraints of bet-hedging are suspiciously absent. Here we extend these ideas to our framework, defining costs based on reaction norm shapes and limits based on emergent strategies. We see *maintenance costs* (including *genetic costs*) as costs of enabling phenotypic variance, and *production costs* as costs arising from the balance of the variance components. In our view production costs include *information acquisition costs* and *instability costs*, but also *stability costs*, that is the additional energetic costs of buffering against noise (see table). The evolutionary limits can be similarly split over the strategy axes: *responsiveness limits* prevent flexible phenotypes, and include *developmental range* and *epiphenotype limits*. *Information use limits*, on the other hand, prevent bet-hedging due to *information reliability* and *lag-time limits*. We hope that this extension of costs and limits to the plasticity – bet-hedging continuum will stimulate further research on the evolvability of plasticity and bet-hedging.

Costs and limits of evolutionary strategies.

Cost type	**Subtype**	**Direction**	**Limit type**	**Subtype**	**Direction**
Maintenance	Genetic	High sum	Responsiveness	Developmental range	Flexible
Production	Information acquisition	σ^2_{among}		Epiphenotype	Flexible
	Instability	σ^2_{within}	Information use	Reliability	Diversified bet-hedging
	Stability	σ^2_{among}		Lag-time	Diversified bet-hedging

Lastly, bet-hedging theory and empirical evidence is based on the special case of entirely unpredictable conditions. For example, the iconic case of desert annuals (Cohen 1966) was chosen precisely because it does not include any interaction with plasticity. One central prediction from this model was that phenotype proportions match exactly the frequency of occurrence of their respective environments (if 20% of the years are bad, the optimal allocation is 20% bad-year specialists and 80% good-year specialists). It appears that this special case means that the elevation of a flat reaction norm depends on the frequency of occurrence, but how this prediction changes with partial phenotypic plasticity is unknown. We tentatively propose for partially predictable environments that it is the sum of variances which correlates with the frequency of good years, but this prediction remains to be tested in future experiments. Obviously, there are many details in the bet-hedging – plasticity relationship that are yet to be explored (Box 3), but we hope that resolving these three core issues will advance bet-hedging to an equal standing as plasticity in a revised evolutionary synthesis.

Box 3: Outstanding questions

Are there cases of truly continuous, non-binary bet-hedging decisions? If they exist, are there qualitative differences in the $\sigma^2_{among} : \sigma^2_{within}$ trade-off? In binary traits the variance of the reaction norm has a very clear relationship with the slope, causing the close association of bet-hedging and plasticity concepts. Without such a slope – variance relationship, do plasticity and diversified bet-hedging still fall on the same axis? Do the costs and limits of plasticity (box 2) impose limits on trait ranges, such that variance becomes one-sided, causing similar slope-variance relationships as in binary traits?

What is non-adaptive plasticity? Do we require the term “non-adaptive bet-hedging”? Should we split the term into “non-adaptive degree of canalization” and “non-adaptive variance composition”? How do we differentiate non-adaptive variance ratios from microplasticity?

Does climate change promote the evolution of bet-hedging strategies? Given that bet-hedging depends on temporal variation of environments, how quickly can it evolve?

Does bet-hedging allow for genetic accommodation and assimilation, or are there functional differences to phenotypic variance by plasticity?

Phenotypes are rarely induced by a single environmental cue. How can we integrate the relationship of multiple interacting cues in this concept?

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Conflict of interest disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article.

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