Benefits of phenotypic plasticity for population growth in varying environments

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Phenotypic plasticity refers to the capacity of the same organisms to exhibit different characteristics under varied environmental conditions. A plastic developmental program allows organisms to sense environmental cues in early stages of life and express phenotypes that are better fitted to environments encountered later in life. This is often considered an adaptive strategy for living in varying environments as long as the plastic response is sufficiently fast, is accurate, and is not too costly. However, despite direct costs of maintaining plasticity and producing phenotypes, a fundamental constraint on the benefit of phenotypic plasticity comes from the predictability of the future environment based on the environmental cues received during development. Here, we analyze a model of plastic development and derive the limits within which this strategy can promote population growth. An explicit expression for the long-term growth rate of a developmentally plastic population is found, which can be decomposed into several easily interpretable terms, representing the benefits and the limitations of phenotypic plasticity as an adaptation strategy. This growth rate decomposition has a remarkably similar form to the expressions previously obtained for the bet-hedging strategy, in which a population randomly diversifies into coexisting subgroups with different phenotypes, implying that those evolutionary strategies may be unified under a common general framework.

developmental plasticity | population growth | evolution

Many organisms have the ability to express different phenotypes in response to environmental conditions. Such phenotypic plasticity allows individual organisms to develop appropriate morphological, physiological, or behavioral traits that better fit a particular environment that they encounter. Some remarkable examples are found in animals that show distinctive polyphenism (1, 2). For instance, different generations of butterfly (e.g., *Araschnia levana*) may develop alternative color patterns on their wings, known as the spring and the summer forms, depending on which season they emerge from pupa (3). Water fleas (*Daphnia*) can grow large helmets and spikes in defense against predators—a response induced by predator cues, such as the concentration of kairomones in the water (4). More remarkably, the tadpoles of certain spadefoot toads (*Spea*), which live in desert areas and breed in temporary ponds filled by rain, can become carnivorous and even cannibalistic to facilitate early metamorphosis if they sense that the pond is drying out (5).

Such phenotypic plasticity can be considered as an evolutionary strategy for adapting to variable environments. To overcome the uncertainty of the environment, juvenile organisms may rely on environmental cues sensed during their development to guide the expression of phenotypes that have a better chance of surviving in the environment that they encounter as adults. Such a "plastic strategy" is useful if the environmental cues are reliable and if the plastic response is not too costly. Several types of costs and limits of phenotypic plasticity have been discussed in the literature (6, 7). Among the most important ones are the costs connected with the extended period often necessary for development and with unexpected changes of the environment during or after this time, which may render the expressed phenotype maladapted.

For unpredictable stochastic environmental variations, an alternative strategy of adaptation is bet hedging. In its extreme form, the population does not need to sense the environmental cues: it may randomly diversify into coexisting subpopulations of different phenotypes so that one of them will have the chance to survive. This bet-hedging strategy has been extensively studied from both experimental and theoretical points of view (8–16). One of the general quantitative results found in these studies is that the limit to which bet hedging can promote long-term population growth is given by the amount of information that the organisms can extract from the environment (*Discussion*).

Here, we study an analogous problem for the plastic strategy. That is, in a stochastically varying environment, how much can the growth of a population benefit from phenotypic plasticity? We also address related questions: for example, what is the optimal form of the plastic response? We answer these questions by considering a simple but general model and by deriving within its framework a fundamental limit to the benefit of phenotypic plasticity in terms of population growth rate. Finally, we compare our results with those for the bet-hedging strategy and reveal an interesting similarity between them.

Model

Consider an organism that undergoes a plastic developmental process over a finite time and expresses an adult phenotype that is then irreversible for the rest of the life. During its developmental stage, the juvenile organism receives certain cues about

Significance

Biological organisms show amazing abilities to change their forms and behavior according to their surroundings. For example, some caterpillars mimic flowers or twigs of the tree depending on their diet, freshwater snails grow thickened and deformed shells on sensing predator cues, and female aphids develop wings for migration if their habitat is crowded. Such flexibility in developing distinct external characteristics is known as "phenotypic plasticity," often considered an adaptation strategy for surviving in variable environmental conditions. The prevalence of this phenomenon calls for a theoretical quantitative understanding of its evolutionary benefits. We use a simple model to illustrate how such benefits can be defined in terms of population growth rate and classify different contributions and limitations to those benefits.

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the environment, such as the temperature, the photoperiod, or the close presence of predators at the time. These environmental cues may influence the course of development that determines the phenotypic traits of the adult organism, such as the body size, the wing color, or the quality of defensive organs. After reaching maturity, the adult organism will encounter an environment, which could be different from the one that it experienced during development. This may happen, for example, if the organism migrates to a new habitat as an adult or if the environment itself changes over time. The condition of the environment that the organism encounters as an adult will affect the number of offspring that it can produce. Those organisms that can better anticipate their future environment and express a favorable phenotype during development will be able to produce more offspring in adulthood. In the long term, such organisms will reach greater abundance and are more likely to be evolutionarily successful.

We will model such developmentally plastic organisms as follows. Let the environmental cue that the organism receives during development be denoted by ξ, and let the phenotype that the organism expresses as an adult be denoted by ϕ. Both of these quantities are in general high-dimensional vectors, with different components representing different environmental factors sensed by the organism and different quantitative traits characterizing the organism, respectively. The expressed phenotype ϕ will depend on the environmental cue ξ as a result of the organism's developmental program. Such dependence will be summarized by a function $\phi = \Phi(\xi)$, which will be called the "plastic response" of the organism. Furthermore, the environment that the organism encounters as an adult will be denoted by ε. In that environment, the number of offspring that the organism can produce is given by a function $f(\phi;\varepsilon)$, which is a measure of fitness. We assume that the environment ε randomly switches between a set of conditions labeled by a superscript μ. Each environment ε^μ favors a particular phenotype ψ^μ, such that the fitness of the organism in ε^μ depends on how close its phenotype ϕ is to the favored phenotype ψ^μ. For simplicity, we assume that $f(\phi;\varepsilon)$ is a Gaussian function, $f(\phi;\varepsilon^\mu) = f^\mu\,\mathrm{e}^{-\gamma^2(\phi-\psi^\mu)^2}$, where f^μ is the maximum number of offspring in each environment ε^μ and $(\cdots)^2$ is the squared distance between the phenotypes. The parameter γ measures the selection pressure ($1/\gamma$ provides a unit for the distance between phenotypes); for brevity, we set $\gamma = 1$ without loss of generality. We consider asexual reproduction, although the model can be extended to sexually reproducing organisms; we also neglect potential parental effects on the phenotype. Our notations are summarized in Table 1.

Our goal is to analyze the growth rate of a population of such organisms. Their generations are assumed to be discrete and largely synchronized, which is the case for many animals that breed in a particular season each year and plants that germinate and flower annually. Each generation is labeled by a number t. For now, we ignore phenotypic variation among individuals of the same generation (a more general case is in *Materials and Methods*). Therefore, in each generation, all individuals will have the same fitness, $f(\phi_t;\varepsilon_t)$, where $\phi_t = \Phi(\xi_t)$. For a large population with demographic fluctuations that can be neglected, the growth of the population size N during that generation will be given by $N_{t+1} = N_t\, f(\phi_t;\varepsilon_t)$. Over many generations, $t = 0, 1, \ldots, T$, the long-term growth rate (LGR) of the population will be (derivation is in *Materials and Methods*)

$$\Lambda = \frac{1}{T}\log\frac{N_T}{N_0} = \sum_{\xi,\varepsilon} P(\xi,\varepsilon)\log f(\Phi(\xi);\varepsilon). \qquad \textbf{[1]}$$

Here, we denote by $P(\xi)$ the probability of occurrence of a particular environmental signal ξ received at the time of development and by $P(\varepsilon)$ the probability of occurrence of a particular environmental condition ε at the time of selection; then, $P(\xi,\varepsilon)$ is the joint probability that both the environmental cue ξ and the environmental condition ε occur together in the same generation.

Results

Solving our simple model of a developmentally plastic population growing in a stochastically varying environment, we obtain an explicit expression for the LGR Λ. This expression can be decomposed into four easily interpretable terms (derivation is in *Materials and Methods*):

$$\Lambda = \Lambda_{\max} - \mathbb{V}[\psi] + \mathbb{V}\left[\mathbb{E}[\psi \mid \xi]\right] - d^2(\Phi^*,\Phi), \qquad \textbf{[2]}$$

which represents

$$\begin{aligned}(\mathrm{LGR}) = {} & (\text{maximum possible growth rate})\\ & - (\text{cost of environmental uncertainty})\\ & + (\text{benefit of phenotypic plasticity})\\ & - (\text{cost of suboptimal plasticity}).\end{aligned}$$

- The first term, $\Lambda_{\max} \equiv \sum_\mu P(\varepsilon^\mu)\log f^\mu$, represents the fastest possible growth rate for any population. This maximum growth rate could only be achieved by organisms with the phenotype that matches the environment perfectly. Such organisms would always make a right choice at the time of development to express the phenotype ψ^μ if the environment at the time of selection is ε^μ. This type of development can be called "perfect anticipation," which would require that the organism could fully predict the future environment at the time of development.
- The second term, $\mathbb{V}[\psi]$, is the variance of the favored phenotype ψ due to environmental variations. Such environmental variations will reduce the growth rate of a population. For organisms with development that is nonplastic (i.e., individuals that express the same predetermined phenotype regardless of the environmental cues), the maximum growth rate is given by the difference of the first two terms: $\Lambda_{\mathrm{bnp}} \equiv \Lambda_{\max} - \mathbb{V}[\psi]$. The greater is the variance of the favored phenotype, the larger is the reduction of growth rate in the absence of phenotypic plasticity.
- The third term, $\mathbb{V}[\mathbb{E}[\psi \mid \xi]]$, is connected with the correlation between the environmental cue ξ received during development and the favored phenotype ψ at the time of selection. This term represents the "benefit of phenotypic plasticity" that helps to increase the LGR of a population. As long as the environmental cue is correlated with—and thus, potentially informative about—the favored phenotype, phenotypic plasticity can be beneficial. However, since the correlation between the environmental cue and the favored phenotype can rarely be perfect, the benefit of phenotypic plasticity would generally not be able to bring the population growth rate to the value $\Lambda_{\max}$. For a given degree of such correlation, the maximum growth rate of a developmentally plastic population is given by

Table 1. Main symbols used in the model

Symbol	Meaning
ξ	Environmental cue received during development
ε	Environment at the time of selection
ϕ	Phenotype expressed by the adult organism
ψ	Favored phenotype in a given environment
Φ	Plastic response: a function that maps cues to phenotypes
γ	Parameter controlling the strength of selection pressure
σ	Parameter controlling the noisiness of environmental cue

the total of the first three terms: $\Lambda^* \equiv \Lambda_{\max} - \mathbb{V}[\psi] + \mathbb{V}[\mathbb{E}[\psi \mid \xi]]$. The "optimal plastic response," which yields the growth rate Λ^*, is denoted by $\Phi^*(\xi)$ and will be described below.

- The last term, $d^2(\Phi^*, \Phi) \equiv \sum_\xi P(\xi)(\Phi^*(\xi) - \Phi(\xi))^2$, measures the difference between the optimal plastic response Φ^* and the actual response Φ used by a population. Because of possible physical constraints, such as a limited range of phenotypes that the developmental program can produce, the organisms may not be able to exactly implement the optimal plastic response. As a result, the population growth rate, Λ, will be lower than the optimal value Λ^*. Hence, this last term represents the loss of population growth rate due to the use of a suboptimal plastic response.

The above decomposition of the population growth rate summarizes the main result of this paper. The relation between those terms is illustrated schematically in Fig. 1. It shows that a population using an optimal plastic response can, in general, achieve faster growth than being nonplastic but not faster than having phenotypes perfectly matched to the environment at all times. The optimal plastic response yields perfectly matched phenotypes only when the environmental cue received by the organism during development is fully predictive of the future environment that it encounters as an adult, in which case the population achieves the maximum growth rate $\Lambda_{\max}$. However, being nonplastic is the optimal response if the environmental cue is not informative about the future environment at all, in which case the population can only grow at a lower rate Λ_{bnp}. Somewhere in between these two limits is the realistic case where information extracted from the environment during development is partially predictive of the future, which allows the population with optimal plasticity to grow at an intermediate rate Λ^*. Finally, although a population using a suboptimal plastic response will grow slower than Λ^*, it is still better than being totally nonplastic if Λ is greater than Λ_{bnp}. In that case, the difference between those two terms can be called the "achieved" benefit of phenotypic plasticity, as indicated in Fig. 1.

The key point in deriving the above results (details are in *Materials and Methods*) is to find the optimal plastic response, Φ^*, that maximizes the value of Λ in Eq. **1**. This can be done by setting the variation of Λ over $\Phi(\xi)$ to zero, which yields

$$\Phi^*(\xi) = \sum_\mu P(\varepsilon^\mu \mid \xi)\psi^\mu \equiv \mathbb{E}[\psi \mid \xi]. \qquad \textbf{[3]}$$

Here, $P(\varepsilon^\mu \mid \xi)$ is the conditional probability of encountering the environment ε^μ at adulthood when the cue ξ is received during development. This expression implies that the optimal plastic response takes the form of Bayesian inference—given the environmental cue ξ, the organism has to effectively estimate the posterior probability of each environment ε^μ and take the average of the favored phenotypes ψ^μ accordingly. If the environmental cue is informative enough to single out the environment that will occur, then the expressed phenotype will be perfectly matched to that environment. Otherwise, a compromise is made between all possible environments that may be encountered.

As an example, consider fruit flies (*Drosophila*), which have larvae that develop in rotting fruits and adults that migrate by air. An important phenotype of the adult fly is the ratio of wing and thorax sizes, which affects the flight capability in a given air condition—the colder the air, the better it is to have a large wing to thorax ratio (17, 18). This phenotype is plastic and depends on the temperature under which the larvae develop (17, 19). In this case, the temperature of the rotting fruit provides an environmental cue received during development, ξ, and the temperature of the air serves as a proxy for the environmental condition of the adult, ε. The environment ε can vary over a wide range, and the favored phenotype ψ is a decreasing function of ε.

To study the optimal plastic response in this case, let us assume that the favored phenotype ψ is a linear function of the environment ε: $\psi(\varepsilon) = a - b\,\varepsilon$. The slope b here characterizes the perfect level of plasticity for the organism. For simplicity, we assume that the environment ε follows a normal distribution, $\mathcal{N}(0, \delta^2)$, and the cue ξ is normally distributed around ε with an SD of σ. Using Eq. **3**, we find that the optimal plastic response is given by $\Phi^*(\xi) = a - \rho\, b\, \xi$, where $\rho = \delta^2/(\delta^2 + \sigma^2)$. This is also a linear function, but the slope is reduced by a factor ρ, which characterizes the correlation between ε and ξ (Fig. 2*A*) (similar theoretical results were found in, for example, refs. 20 and 21). This example clearly illustrates that the optimal level of phenotypic plasticity depends on the amount of correlation between the environment of the adult and the cue received during development. If they are not fully correlated, $\rho < 1$, then the slope of the optimal plastic response will be smaller than that of the favored phenotype. This is found to be the case for the plastic wing to thorax ratio of *Drosophila melanogaster* with respect to temperature, which is attributed to the lack of correlation between the temperatures at development and selection (20).

An important feature of the optimal plastic response is that, when the environmental cue received during development is noisy, the plastic response would be robust against such noise. This feature is best observed in cases where the environmental conditions are discrete. As an example, consider butterflies

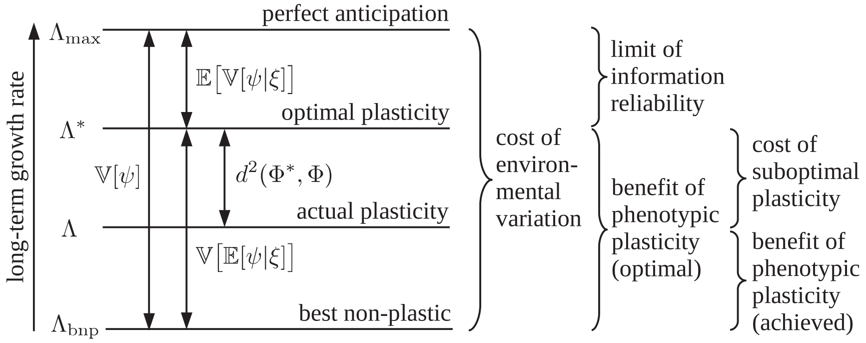

Fig. 1. Decomposition of the long-term population growth rate Λ. The growth rates of the perfectly anticipating population ($\Lambda_{\max}$), the best nonplastic population (Λ_{bnp}), the optimally plastic population with given environmental cues (Λ^*), and an actual population with suboptimal plasticity (Λ) are drawn as lines at different heights. Λ^* is in between $\Lambda_{\max}$ and Λ_{bnp}; it approaches $\Lambda_{\max}$ if the environmental cue received during development is fully predictive of the favored phenotype at the time of selection and approaches Λ_{bnp} when the environmental cue is not informative about the favored phenotype at all. Moreover, Λ is below Λ^* if the plastic response is suboptimal; phenotypic plasticity is still beneficial if Λ is above Λ_{bnp}.

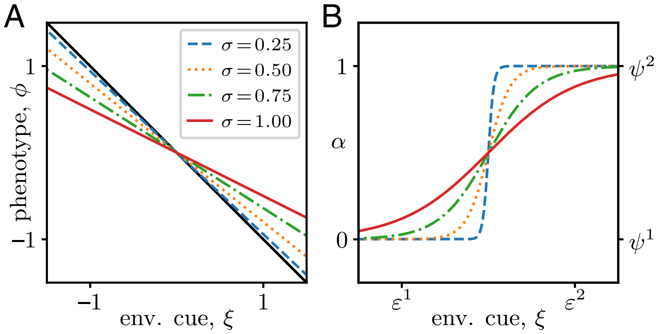

Fig. 2. Examples of optimal plastic responses. (*A*) The environment ε has a normal distribution $\mathcal{N}(0, 1)$; the environmental cue ξ is normally distributed around ε with an SD of σ. The favored phenotype ψ is a linear function of ε with a negative slope (normalized to one; black line). The optimal plastic response has a reduced slope, since for $\sigma > 0$, the cue ξ is not fully correlated with the environment ε. (*B*) There are two discrete environments, $\varepsilon^{1,2} = \pm 1$, which occur with equal probability; the environmental cue ξ is normally distributed around ε^μ with an SD of σ, which measures the size of random noise (*A*). The optimal plastic response varies in between the favored phenotypes ψ^1 and ψ^2, with a sigmoidal shape that is robust to noise around ε^1 and ε^2.

(*Bicyclus anynana*) living in a seasonal environment with distinct dry and wet seasons. Alternative seasonal forms, differing in wing pattern, relative abdomen mass, metabolic rate, etc. can be induced by the temperature during larval development (22, 23). Those phenotypic traits will affect the survival and breeding success of adult butterflies. For instance, in the warm wet season, prominent eyespots on the ventral wings of *B. anynana* help to deflect predator attacks, whereas in the cool dry season, reduced color patterns provide better camouflage (22). To develop the correct seasonal form, the larvae would sense the temperature during development to help distinguish which season they will emerge in as adults. However, the temperature fluctuates over time and introduces noise in the received signal. Therefore, the developmental program must be plastic yet, at the same time, robust to the environmental noise.

Such robustness is implied by our model. Let us denote the environmental conditions of the dry and wet seasons by ε^1 and ε^2, respectively, which could represent relatively low and high temperatures. The favored phenotypes in those environments are denoted by ψ^1 and ψ^2, respectively, which may represent less or more prominent wing patterns as well as other dimorphic traits. The environmental cue ξ will represent the temperature at the time of development, which correlates with the season during which the adults emerge and breed. For simplicity, we assume that ε^1 and ε^2 are equally likely and that ξ has a normal distribution centered around either ε^μ, with an SD of σ representing the level of environmental noise. According to Eq. **3**, the optimal plastic response is $\Phi^*(\xi) = (1-\alpha)\psi^1 + \alpha\,\psi^2$, where α as a function of ξ is plotted in Fig. 2*B*. It can be seen that, for a relatively low noise level, the response function has a sharp sigmoidal shape. As a result, the relatively flat regions near ε^1 and ε^2 are robust to noise in the environmental cue ξ, whereas the steep region in the middle is sensitive to signal changes and leads to a plastic response. For high levels of noise, however, the plastic response becomes more smooth and linear within the environmental range between ε^1 and ε^2. Such sigmoidal shape, with various degrees of smoothness, has been observed for the aforementioned phenotypic traits of *B. anynana* (23).

Discussion

Our main result (Eq. **2**) is reminiscent of a similar decomposition of the LGR for a population using a bet-hedging strategy while receiving environmental information (9, 15). In that model, the population diversifies into coexisting groups of distinct phenotypes described by a phenotype distribution $\pi(\phi\,|\,\xi)$ that may depend on the received environmental cue ξ. It is assumed that the environment switches between a set of conditions, $\{\varepsilon^\mu\}$, each associated with a favored phenotype ψ^μ; however, in contrast to our model, the phenotype ϕ that an organism expresses is selected only from the set $\{\psi^\mu\}$, and the organism survives only if its phenotype exactly matches the favored phenotype for the present environment. Under those assumptions, it has been found that the LGR of the population is given by (equation 23 in ref. 15)

$$\Lambda = \Lambda_{\max} - H(\psi) + I(\psi;\xi) - D(\pi^*\|\pi). \qquad \textbf{[4]}$$

The term $\Lambda_{\max}$ represents the maximum population growth rate, which can only be achieved by organisms that express the environmentally favored phenotype at all times, the same as in our model. The term $H(\psi)$ is the entropy of the favored phenotype ψ or, equivalently, that of the environment ε. It measures the intrinsic uncertainty of the environment and the favored phenotype, which reduces the population growth rate, similar to the term $\mathbb{V}[\psi]$ in our model. The term $I(\psi;\xi)$ is the mutual information between the favored phenotype ψ and the environmental cue ξ, which is a measure of their correlation, similar to the term $\mathbb{V}[\mathbb{E}[\psi\,|\,\xi]]$ in our model. For a bet-hedging population that uses environmental information, this term is interpreted as the "value of information" in promoting long-term population growth. Finally, the term $D(\pi^*\|\pi)$ is the relative entropy between the optimal phenotype distribution π^* and the actual distribution π, which measures the difference between the two distributions. This term represents the cost of using a suboptimal bet-hedging strategy, analogous to the term $d^2(\Phi^*, \Phi)$ in our model for a suboptimal plastic strategy.

The strong resemblance between Eqs. **2** and **4** suggests a close connection between the two adaptation strategies of plastic development and bet hedging. Indeed, a bet-hedging strategy that uses environmental information to alter the phenotype distribution can be viewed as a type of plasticity—not only the phenotype is plastic (since individuals of an isogenic population can develop different phenotypes), but the distribution of phenotypes (or the propensity of each individual to express different phenotypes) is also plastic and depends on environmental cues. In contrast, a purely bet-hedging population that does not rely on environmental information is analogous to a nonplastic population with an LGR that is limited by the environmental uncertainty, as expressed by the first two terms of the growth rate decomposition [**4**]. From this perspective, the third term representing the value of environmental information may also be viewed as the benefit of plasticity provided by the amount of correlation between the received environmental cue and the favorable phenotype.

The fact that both models of phenotypic plasticity and bet hedging, under different assumptions, give rise to the same form of growth rate decomposition hints that they could be unified under the same theoretical framework. Indeed, an environmentally dependent bet-hedging strategy can be biologically realized by coupling a plastic developmental program to an environmental cue that varies between individuals (more details are in *Materials and Methods*). Although the particular expression for the population growth rate will depend on the detailed assumptions of the model, the existence and the meaning of the terms in the growth rate decomposition will generally be independent of such details. Those terms can be defined, in principle, as the differences between the LGRs of the perfectly anticipating population ($\Lambda_{\max}$), the best nonplastic population (Λ_{bnp}), the optimally plastic population under given environmental cues (Λ^*), and the actual population with a certain level of phenotypic plasticity (Λ). The relation between those terms can, in general, be depicted by a diagram similar to the one shown in Fig. 1.

Conceptually, the terms in the growth rate decomposition can be associated with various types of constraints of phenotypic plasticity discussed in the literature (6). For example, the difference between $\Lambda_{\max}$ and Λ^* can be interpreted as the "information reliability limit" of phenotypic plasticity, since it is caused by the incomplete correlation between the environment and the cue. Similarly, the term $d^2(\Phi^*, \Phi)$ that measures the difference between Λ^* and Λ can be interpreted as the "developmental range limit" of phenotypic plasticity, since it is caused by the inability of the developmental process to produce the optimal phenotypic response. Moreover, the optimal plastic response $\Phi^*(\xi)$, given by Eq. **3**, is undetermined for a vanishing $P(\xi)$ (i.e., for environmental cues that rarely occur); this may represent the situation where the organism encounters extreme environments under which it could develop abnormal phenotypes. This would give rise to the problem of "developmental instability," another type of constraint for phenotypic plasticity (6).

Note that, in our simple model, we did not include direct costs of plasticity, such as "maintenance" and "production" costs associated with sensory and regulatory machineries for expressing plastic phenotypes. It is expected that phenotypic plasticity is overall adaptive if its growth benefit outweighs these costs. By deriving the fundamental limit to the benefit of phenotypic plasticity, we effectively put a bound on the cost of plasticity that allows phenotypic plasticity to emerge through evolution.

Materials and Methods

Derivation of Population Growth Rate. Recall that, in our model, ξ is the environmental cue that an organism receives during development and that ε is the environmental condition that it encounters as an adult. The phenotype of the organism is determined by a plastic response function, $\phi = \Phi(\xi)$, and the expected number of offspring is determined by a fitness function, $f(\phi; \varepsilon)$. We denote by $P(\xi, \varepsilon)$ the joint probability distribution of ξ and ε.

Neglecting phenotypic variation between individuals and demographic fluctuation of the population, the population size N will grow in every generation t according to

$$N_{t+1} = N_t\, f(\phi_t; \varepsilon_t), \quad \text{where} \quad \phi_t = \Phi(\xi_t). \qquad \textbf{[5]}$$

Both ξ_t and ε_t may vary over time, with possible correlation between them. The LGR of the population can be formally defined as

$$\Lambda \equiv \lim_{T\to\infty} \frac{1}{T} \log \frac{N_T}{N_0}. \qquad \textbf{[6]}$$

Using Eq. **5** in the above definition, one finds that

$$\Lambda = \lim_{T\to\infty} \frac{1}{T} \sum_{t=0}^{T-1} \log f(\Phi(\xi_t); \varepsilon_t). \qquad \textbf{[7]}$$

It can be considered as the time average of the per generation growth rate $\log f(\Phi(\xi_t); \varepsilon_t)$. In the long term, the time average can be replaced by a probability average, yielding

$$\Lambda = \sum_{\xi,\varepsilon} P(\xi, \varepsilon) \log f(\Phi(\xi); \varepsilon). \qquad \textbf{[8]}$$

Specializing to the case where the fitness is given by a Gaussian function $f(\phi; \varepsilon) = f(\varepsilon)\, \mathrm{e}^{-\gamma^2(\phi - \Psi(\varepsilon))^2}$, where $f(\varepsilon)$ is the maximum fitness and $\Psi(\varepsilon)$ is the favored phenotype (both being functions of the environment ε), the LGR becomes

$$\Lambda = \sum_{\varepsilon} P(\varepsilon) \log f(\varepsilon) - \gamma^2 \sum_{\xi,\varepsilon} P(\xi, \varepsilon)(\Phi(\xi) - \Psi(\varepsilon))^2. \qquad \textbf{[9]}$$

Note that γ and Λ have the units of (phenotype unit)$^{-1}$ and (generation number)$^{-1}$, respectively. If we label different ε by ε^μ and denote $f(\varepsilon^\mu) = f^\mu$ and $\Psi(\varepsilon^\mu) = \psi^\mu$, then

$$\Lambda = \sum_{\mu} P(\varepsilon^\mu) \log f^\mu - \gamma^2 \sum_{\xi,\mu} P(\xi, \varepsilon^\mu)\left(\Phi(\xi) - \psi^\mu\right)^2. \qquad \textbf{[10]}$$

Solution of Optimal Plastic Response. To find the optimal plastic response Φ^*, we take the variation of Λ with respect to $\Phi(\xi)$:

$$\frac{\delta \Lambda}{\delta \Phi(\xi)} = -2\gamma^2 \sum_{\mu} P(\xi, \varepsilon^\mu)\left(\Phi(\xi) - \psi^\mu\right). \qquad \textbf{[11]}$$

Setting this variation to zero leads to the equation

$$P(\xi)\Phi(\xi) = \sum_{\mu} P(\xi, \varepsilon^\mu)\psi^\mu. \qquad \textbf{[12]}$$

Solving this equation yields

$$\Phi^*(\xi) = \sum_{\mu} P(\varepsilon^\mu \mid \xi)\psi^\mu \equiv \mathbb{E}[\psi \mid \xi], \qquad \textbf{[13]}$$

where we used Bayes' rule to find the conditional probability distribution, $P(\varepsilon^\mu \mid \xi) = P(\xi, \varepsilon^\mu)/P(\xi)$, and $\mathbb{E}[\psi \mid \xi]$ denotes the conditional mean of ψ for a given ξ. Note that $P(\varepsilon^\mu \mid \xi)$ is undefined for those ξ that have $P(\xi) = 0$; hence, $\Phi^*(\xi)$ is obtained only for environmental cues that occur. Since the coefficients, $P(\varepsilon^\mu \mid \xi)$, are nonnegative and sum to one, the resultant phenotype $\Phi^*(\xi)$ is inside the convex polytope formed by $\{\psi^\mu\}$ as vertices in the phenotype space.

Decomposition of LGR. We can decompose the value of Λ from Eq. **10** as follows (setting $\gamma = 1$ for brevity):

$$\begin{aligned}\Lambda &= \sum_{\mu} P(\varepsilon^\mu) \log f^\mu - \sum_{\xi,\mu} P(\xi, \varepsilon^\mu)\left[\left(\psi^\mu - \mathbb{E}[\psi \mid \xi]\right) + \left(\mathbb{E}[\psi \mid \xi] - \Phi(\xi)\right)\right]^2 \\ &= \sum_{\mu} P(\varepsilon^\mu) \log f^\mu - \sum_{\xi} P(\xi) \sum_{\mu} P(\varepsilon^\mu \mid \xi)\left(\psi^\mu - \mathbb{E}[\psi \mid \xi]\right)^2 \\ &\quad - \sum_{\xi} P(\xi)\left(\mathbb{E}[\psi \mid \xi] - \Phi(\xi)\right)^2. \end{aligned} \qquad \textbf{[14]}$$

The first term is the maximum possible value of Λ, which is denoted by $\Lambda_{\max}$. The second term is the conditional variance of ψ given ξ and then averaged over ξ, which is denoted by $\mathbb{E}[\mathbb{V}[\psi \mid \xi]]$; this term can be further decomposed using the law of total variance as $\mathbb{E}[\mathbb{V}[\psi \mid \xi]] = \mathbb{V}[\psi] - \mathbb{V}[\mathbb{E}[\psi \mid \xi]]$. The last term is the only term that depends on $\Phi(\xi)$, from which it is clear that $\Phi^*(\xi) = \mathbb{E}[\psi \mid \xi]$; this term defines a squared distance between the functions $\Phi^*(\xi)$ and $\Phi(\xi)$, which is denoted by $d^2(\Phi^*, \Phi)$. Putting all terms together, we find

$$\Lambda = \Lambda_{\max} - \mathbb{V}[\psi] + \mathbb{V}\left[\mathbb{E}[\psi \mid \xi]\right] - d^2(\Phi^*, \Phi), \qquad \textbf{[15]}$$

which is the growth rate decomposition (Eq. **2**).

Now consider a nonplastic population with individuals that always express a predetermined phenotype regardless of environmental cues. Such a nonplastic response can be described by $\Phi(\xi) = \phi_0$ for all ξ, where ϕ_0 is a constant phenotype. Then, the LGR (Eq. **10**) becomes

$$\Lambda = \sum_{\mu} P(\varepsilon^\mu) \log f^\mu - \sum_{\mu} P(\varepsilon^\mu)\left(\phi_0 - \psi^\mu\right)^2. \qquad \textbf{[16]}$$

Maximizing the above value of Λ with respect to ϕ_0 yields the best nonplastic phenotype, $\phi_0^* = \sum_\mu P(\varepsilon^\mu)\psi^\mu = \mathbb{E}[\psi]$. Accordingly, the maximum growth rate for the nonplastic population is

$$\Lambda_{\mathrm{bnp}} = \Lambda_{\max} - \sum_{\mu} P(\varepsilon^\mu)\left(\psi^\mu - \mathbb{E}[\psi]\right)^2 = \Lambda_{\max} - \mathbb{V}[\psi], \qquad \textbf{[17]}$$

the first two terms of the decomposition (Eq. **15**).

Moreover, the maximum growth rate for a plastic population is given by inserting the optimal plastic response $\Phi^*(\xi)$ into Eq. **10**, which yields

$$\Lambda^* = \Lambda_{\max} - \mathbb{V}[\psi] + \mathbb{V}\left[\mathbb{E}[\psi \mid \xi]\right] = \Lambda_{\mathrm{bnp}} + \mathbb{V}\left[\mathbb{E}[\psi \mid \xi]\right]. \qquad \textbf{[18]}$$

This corresponds to the first three terms of Eq. **15** as can be expected, since the last term $d^2(\Phi^*, \Phi)$ vanishes when $\Phi = \Phi^*$. Note that Λ^* always is in between $\Lambda_{\max}$ and Λ_{bnp} (i.e., $\Lambda_{\max} \geq \Lambda^* \geq \Lambda_{\mathrm{bnp}}$), because the term $\mathbb{V}[\mathbb{E}[\psi \mid \xi]]$ satisfies $0 \leq \mathbb{V}[\mathbb{E}[\psi \mid \xi]] \leq \mathbb{V}[\psi]$. The upper limit $\Lambda^* = \Lambda_{\max}$ is reached only when $\mathbb{V}[\psi] - \mathbb{V}[\mathbb{E}[\psi \mid \xi]] = \mathbb{E}[\mathbb{V}[\psi \mid \xi]] = 0$; this happens if $\mathbb{V}[\psi \mid \xi] = 0$ for all

ξ (i.e., when ψ is fully determined by ξ). It means that the optimal plastic response is perfect when the environmental cue can help to single out the favored phenotype. The lower limit $\Lambda^* = \Lambda_{\text{bnp}}$ is reached when $\mathbb{V}[\mathbb{E}[\psi \mid \xi]] = 0$, which happens if $\mathbb{E}[\psi \mid \xi]$ does not vary with ξ; this is the case when ξ is totally irrelevant for predicting ψ. It means that, when the environmental cue is not informative at all, the optimal response is to be nonplastic.

Generalization to Individual Variations. So far, we have ignored phenotypic variation among individuals of the same generation. It was assumed that they receive the same environmental cue ξ that determines their phenotype. This environmental cue can be thought to represent the macroenvironment shared by all individuals that undergo development around the same time.

Now consider the case where, on top of such macroenvironment ξ, each individual experiences a unique microenvironment, ζ, during development. We assume that, for a given macroenvironment ξ, the microenvironment ζ varies among individuals according to a conditional probability distribution $P(\zeta \mid \xi)$. An organism experiencing a microenvironment ζ will develop a phenotype $\phi = \Phi(\zeta)$. In that case, instead of Eq. **8**, the LGR of the population will be given by

$$\Lambda = \sum_{\xi,\varepsilon} P(\xi, \varepsilon) \log \sum_{\zeta} P(\zeta \mid \xi) f(\Phi(\zeta); \varepsilon). \qquad \mathbf{[19]}$$

For a fitness function given by $f(\phi; \varepsilon) = f(\varepsilon)\, \mathrm{e}^{-\gamma^2(\phi - \Psi(\varepsilon))^2}$ as before, the LGR becomes

$$\Lambda = \sum_{\varepsilon} P(\varepsilon) \log f(\varepsilon) - \sum_{\xi,\varepsilon} P(\xi, \varepsilon) \log \sum_{\zeta} P(\zeta \mid \xi) \mathrm{e}^{-\gamma^2(\Phi(\zeta) - \Psi(\varepsilon))^2}. \qquad \mathbf{[20]}$$

The optimal plastic response will be determined by the equation $\delta\Lambda/\delta\Phi(\zeta) = 0$, which, unfortunately, does not have an explicit solution in this case. To find the optimal plastic response, Φ^*, one could use numerical methods instead.

Relation to Bet-Hedging Model. The expression of the LGR in the presence of individual variations (Eq. **19**) bears a strong resemblance to that in a model of bet hedging with environmental information (15). To see the connection, we can define a phenotype distribution among the population by

$$\pi(\phi \mid \xi) \equiv \sum_{\zeta} P(\zeta \mid \xi) \delta(\phi, \Phi(\zeta)), \qquad \mathbf{[21]}$$

where $\delta(x, y)$ denotes the delta function that vanishes unless $x = y$. Then, the LGR can be expressed as

$$\Lambda = \sum_{\xi,\varepsilon} P(\xi, \varepsilon) \log \sum_{\phi} \pi(\phi \mid \xi) f(\phi; \varepsilon). \qquad \mathbf{[22]}$$

This is the same equation that describes the LGR in the model of bet hedging, with ξ playing the role of acquired information about the environmental state. In the bet-hedging model, the phenotype variation described by the distribution π is often assumed to arise from stochastic processes inside individual organisms. In our model of phenotypic plasticity, however, the phenotype variation is generated by coupling a deterministic developmental program Φ to a variable external signal ζ.

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