Evolutionary Ecology Research, 2014, **16**: 631–647

Environmental variation does not always promote plasticity: evolutionarily realized reaction norm for costly plasticity

Atsushi Yamauchi[1] and Daisuke Takahashi[1,2]

[1]*Center for Ecological Research, Kyoto University, Otsu, Japan and* [2]*Department of Mathematics and Mathematical Statistics, Umeå University, Umeå, Sweden*

ABSTRACT

Question: How does environmental variability influence evolutionarily realized phenotypic plasticity?

Mathematical method: Optimization in a spatially fluctuating environment.

Key assumptions: Either the maintenance cost of plasticity results from the amount of phenotypic response, or it results from the slope of the reaction norm. And there are two alternative types of state-specific benefit functions: either the benefit is maximal at an intermediate phenotype, or it is a monotonically increasing function of phenotype.

Conclusion: Organisms may not respond to rare environmental states. In this case, environmental variability suppresses two indices of phenotypic plasticity, i.e. the range of plasticity and the maximum slope of the reaction norm.

Keywords: environmental fluctuation, model, optimization, phenotypic plasticity.

INTRODUCTION

Phenotypic plasticity is the ability of organisms to develop systematically different phenotypes from a single genotype in different environmental conditions. Phenotypic plasticity is often quantified by the 'reaction norm', a functional relationship between phenotypic values and environmental states (Stearns, 1989; Thompson, 1991; Agrawal, 2001; Pigliucci, 2001; Auld *et al.*, 2010; Scheiner *et al.*, 2012). Such a function represents the ability of a genotype to respond to changing environmental conditions. When the phenotypic response is advantageous for individual organisms, it is referred to as 'adaptive phenotypic plasticity'.

Organisms are considered to have evolved a level of phenotypic plasticity that promotes their success across all possible environmental states. If the plasticity of a phenotype is not restricted by any constraints or costs, organisms may have acquired the ability to construct the best phenotype under each environmental state. Therefore, the reaction norm should

---

Correspondence: A. Yamauchi, Center for Ecological Research, Kyoto University, Hirano 2-509-3, Otsu 520-2113, Japan. e-mail: a-yama@ecology.kyoto-u.ac.jp

link optimal solutions for various environmental states, referred to as the 'optimal reaction norm', which can be considered a straightforward extension of optimization under each given environmental state. In this case, the environmental state can be considered a parameter, under which the organism optimizes its own phenotype. In reality, however, the flexibility of a phenotype may be constrained by many factors (Newman, 1992; DeWitt *et al.*, 1998; Agrawal, 2001; Pigliucci, 2001). DeWitt and colleagues reviewed the potential constraints of phenotypic plasticity and categorized them into two classes: costs of plasticity and limits to the benefits of plasticity (DeWitt *et al.*, 1998). The costs of plasticity involve (1) maintenance costs, (2) production costs, (3) information-acquisition costs, (4) developmental instability costs, and (5) genetic costs. These factors constrain the evolution of phenotypic plasticity, causing the reaction norm to stray far from a set of optimal solutions under each environmental state.

Theoretical approaches to the study of the evolution of phenotypic plasticity have been categorized into three classes: optimality models, gametic models, and quantitative genetic models (Scheiner, 1993; Berrigan and Scheiner, 2004). Quantitative genetic models focus mainly on genetic costs, which are equivalent to the fifth class of plasticity costs above. Van Tienderen analysed the evolution of generalists and specialists within a two-habitat structure using a quantitative genetic model in which generalists were considered to exhibit phenotypic plasticity accompanied by a cost (van Tienderen, 1991, 1997). Scheiner and colleagues examined the joint evolution of phenotypic plasticity and dispersal rate using an individual-based model that also considered the cost of plasticity (Scheiner *et al.*, 2012). However, with a few exceptions, plasticity costs have received limited interest in theoretical studies.

On the other hand, in a theoretical study, Ernande and Dieckmann (2004) used the optimization approach to examine the evolution of the reaction norm within the continuous space of environmental states, while also considering the cost of plasticity. They assumed that the plasticity cost results from a difference between a given baseline phenotype and the reaction norm. Based on this assumption, they successfully revealed the effects of environmental stochasticity, population dynamics, and the cost of plasticity on the evolution of the reaction norm. However, they did not consider factors important for the evolution of phenotypic plasticity, such as the possibility of other definitions of the plasticity cost, or the cost and the evolvability of the baseline phenotype. These factors can substantially influence the form of the reaction norm over the space of environmental states. In particular, if there is a difference in the costs of the baseline phenotype and the plastic response, the evolvability of the baseline phenotype may affect the magnitude of the plastic response.

In the present study, we construct a model of the evolution of phenotypic plasticity and the reaction norm, extending the optimization approach of Ernande and Dieckmann (2004) by considering factors not addressed in their analysis. We then investigate the evolution of the reaction norm, assuming specific conditions for cost and benefit functions, and environmental stochasticity. Based on this analysis, we examine the relationship between the variability of environmental states and evolutionarily realized phenotypic plasticity. Intuitively, one would expect phenotypic plasticity to be promoted by environmental variability, as it is a strategy for adapting to a variable environment. Our analysis, however, indicates that the variability can conditionally suppress phenotypic plasticity.

MATHEMATICAL MODEL

Organisms often alter their own phenotypes discontinuously despite continuous environmental conditions and cues. For example, a high and low density of predators may induce and repress, respectively, the expression of a defensive trait in a prey individual. In this case, the phenotype is binary, whereas the environmental condition (predator density) is a continuous variable. In the present study, we assume that an organism can discretely express at most X types of phenotypes depending on environmental conditions. The spectrum of environmental conditions is classified with respect to the phenotype, which is numbered by a discrete variable x (=1, 2, 3 . . . X). It should be noted that the environmental state x is defined with regard to phenotypic responses. With a fixed x-interval, a larger X allows the organism a finer response to the environment. This definition of environmental state can represent various situations from rough to fine phenotypic plasticity; as X gets larger, the vector tends towards a continuous reaction norm. (However, this definition may make application to empirical studies difficult; see evolutionary-ecology.com/data/2946Appendix.pdf.)

The environmental state has a probability mass function $p(x)$, i.e. a spatial environmental stochasticity (though we analyse a temporally fluctuating environment in the Appendix). An individual will settle in environmental state x with probability $p(x)$, after which it expresses the phenotypic plasticity. An individual is considered to possess the ability to develop different phenotypes, $v(x)$, under different environmental states, x. The phenotypes $v(x)$ consist of two components: a constitutive phenotype, v_c, and an environment-specific plastic response: $v(x) - v_c$. The organism always produces the constitutive phenotype v_c and then additionally develops the plastic response $v(x) - v_c$ in response to an environmental state, x. The vector of $v(x)$ is denoted by $\mathbf{v}$, which is referred to as the reaction norm.

The expressed phenotype will result in both benefits and costs to the individual. The individual benefit can be a function of both the environmental state x and individual phenotype $v(x)$, which is denoted by a state-specific benefit function, $f(x, v(x))$. Under a spatially varying environment, the average benefit for an individual with a reaction norm $\mathbf{v}$ can be formulated as the frequency-weighted average of the state-specific benefit as follows:

$$B(\mathbf{v}) = \sum_{x=1}^{X} p(x) f(x, v(x)). \tag{1}$$

Furthermore, we assume that there is a cost of the reaction norm $\mathbf{v}$. The cost can result from various processes, such as a trade-off with other traits, although we omit details about its mechanism. We formulate the cost that accompanies the reaction norm as

$$C(\mathbf{v}) = k_p \sum_{x=1}^{X} p(x)(v(x) - v_c) + k_c v_c + D(\mathbf{v}), \tag{2}$$

which partly follows definitions in Ernande and Dieckmann (2004). The first term of equation (2) represents an average of the production cost of the plastic response to a given environmental state $(v(x) - v_c)$ with a unit cost to produce the plastic response, k_p. The second term is a production cost of the constitutive phenotype (v_c), the unit cost of which is defined as k_c. The production costs of the plastic response and constitutive phenotype are considered also to involve investments in their maintenance after production. The third term $D(\mathbf{v})$

represents costs that are paid for the potential of being plastic, which is a maintenance cost of phenotypic plasticity. This cost is not denoted explicitly here because we propose two types of formulation for it below. The critical difference between the plasticity production cost and maintenance cost of plasticity $D(\mathbf{v})$ is that the former depends on $p(x)$ whereas $D(\mathbf{v})$ does not. $D(\mathbf{v})$ is the cost of maintaining the ability to produce each plastic response $v(x) - v_c$ if the organism were to encounter the corresponding environment x. It does not depend on the environmental frequencies, $p(x)$. In contrast, the plasticity production cost is the actual cost of producing and maintaining the response $v(x) - v_c$, and it is not incurred until the organism is in environment x; it therefore depends on $p(x)$, since $p(x)$ determines the probability that x is experienced.

We consider that the unit costs of the production of plasticity and the production of the constitutive phenotype can differ from each other (i.e. $k_p \neq k_c$) owing to a difference in the time required to maintain the phenotype between them. The plastic response is expressed only after determination of the environment, whereas the constitutive phenotype may be produced at an early life stage and maintained over the organism's lifetime. For example, plants are known to produce defensive chemicals that are considered to require costs for maintenance (Neilson *et al.*, 2013). In this case, the cost of induced defence (i.e. plastic response to herbivore attack) could be smaller than that of constitutive defence (i.e. constitutive phenotype) due to a shorter maintenance period. Therefore, we assume that the constitutive phenotype can be more costly than the plastic response in terms of production, i.e. $k_p \leq k_c$ in the present analysis (this condition is partly relaxed in the Appendix). If these costs are identical (i.e. $k_p = k_c$), the formulation is similar to that of Ernande and Dieckmann (2004) by cancelling two v_c in equation (2). It should also be noted that when the expressed phenotype in equation (2) is smaller than the constitutive phenotype, the production cost of plasticity in a specific environmental state is negative (i.e. $v(x) - v_c < 0$). This implies that the investment in the constitutive phenotype is partially refunded if the phenotypic value is reduced by a negative plastic response.

Based on the formulations of benefit $B(\mathbf{v})$ and cost $C(\mathbf{v})$, individual fitness is represented by $\phi(\mathbf{v}) = B(\mathbf{v}) - C(\mathbf{v})$, which can be rewritten as:

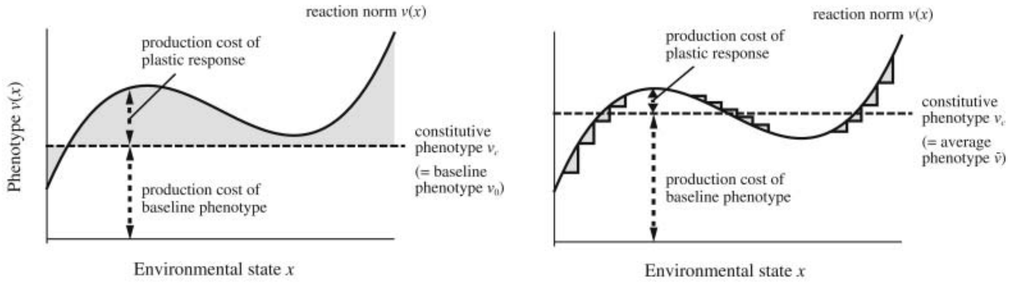
$$\phi(\mathbf{v}) = \sum_{x=1}^{X} p(x)\{f(x, v(x)) - k_p v(x)\} - \{(k_c - k_p)v_c + D(\mathbf{v})\}. \tag{3}$$

Note that the constitutive phenotype v_c disappears in the second term when its production cost corresponds with that of the plastic response ($k_p = k_c$). This is because the production cost of the phenotype does not vary despite its production process, i.e. constitutive or plastic production. Even in such a case, however, the maintenance cost of plasticity, $D(\mathbf{v})$, may still involve the constitutive phenotype, v_c.

In terms of the maintenance cost of plasticity, $D(\mathbf{v})$, we consider two forms. One form reflects a given amount of plastic response in each environmental state (see Fig. 1a). In this case, the cost can be a summation of potential abilities to modify the individual phenotype from the constitutive level to the realized level over the space of environmental states. This may correspond to situations where phenotypic responses are achieved by varying mechanisms depending on environmental states. An alternative type of maintenance cost of plasticity is determined by the slope of the reaction norm over environmental states (see Fig. 1b). If responses to environmental states are realized by tuning physiological pathways or developmental processes of the traits of concern, costs may accompany the

(a) Cost function 1

(b) Cost function 2



(c) Benefit function 1

(d) Benefit function 2

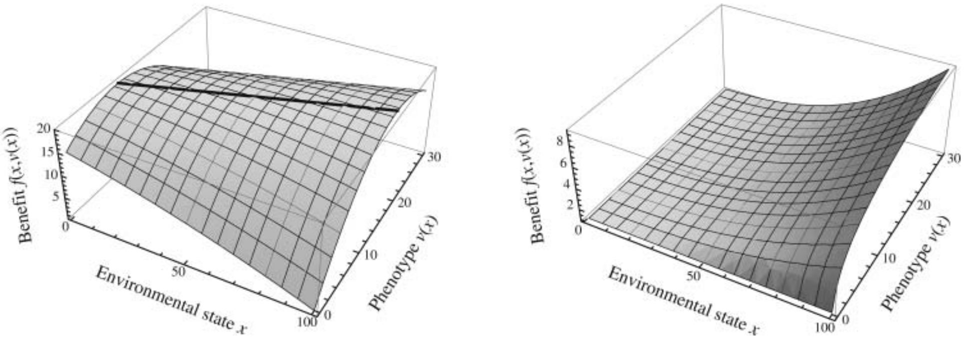


Fig. 1. Panels (a) and (b) show two types of maintenance cost of plasticity that are assumed in the analysis, which are schematically indicated by grey shading. The phenotype is considered to comprise a constitutive phenotype and a plastic response. The constitutive phenotype is accompanied by a production cost only, whereas the plastic response includes a production cost and a maintenance cost of plasticity. In (a), the constitutive phenotype is considered the baseline phenotype, and the maintenance cost of plasticity is a function of the amount of the plastic response. In (b), the constitutive phenotype is considered to be the average (rather than the baseline) phenotype, and the maintenance cost of plasticity is a function of the slope of the reaction norm. Panels (c) and (d) represent two types of state-specific benefit functions that are assumed in the analysis. In (c), benefit is maximized at a beneficial phenotype $w(x)$ under a given environmental state ($f(x, v(x)) = 20 - 0.05(w(x) - v(x))^2$, where $w(x) = 0.1(x - 50) + 15$). The beneficial phenotype $w(x)$ is not an optimal phenotype, because the accompanying costs are defined separately. In (d), benefit is a monotonically increasing function of the phenotype ($f(x, v(x)) = 1 + 0.00002x^{2.5} \log(2v(x) + 1)$).

differentiations of these pathways/processes. In this case, the cost could result from a phenotypic difference between neighbouring environmental states rather than the amount of the phenotypic response itself. These cases are explained in detail and discussed in the Appendix. In reality, phenotypic plasticity could involve the two types of maintenance costs simultaneously, although we treat these separately to clarify the effects of each cost function on the evolutionary process of the reaction norm.

The first model (Model 1) considers the case when the maintenance cost of plasticity is determined by a degree of flexible response over the environmental states (Fig. 1a). The simplest assumption may be that the maintenance cost is proportional to the absolute value of the plastic response, although this makes differentiation of fitness with respect to phenotype difficult. In addition, if we assume that the maintenance cost is proportional to the absolute value of the plastic response, the optimal baseline phenotype would unrealistically diverge to either negative or positive infinity depending on parameters. Thus, the maintenance cost is represented here by the square function of the plastic response, with a cost coefficient, k_m. It should be noted that this cost formation tends to partly correlate with the variance of phenotype, despite its focus on differences from the baseline phenotype rather than differences from the mean value. In this model, we assume that the constitutive phenotype, v_c, can evolve as a strategy of the organism, which is referred to as the baseline phenotype, v_0.

The second model (Model 2) considers a case in which the maintenance cost of plasticity is determined by the slope of the reaction norm over various environmental states (Fig. 1b). The maintenance cost could be simply assumed to be proportional to the absolute value of the slope, although this makes differentiation of fitness with respect to phenotype difficult. Thus, the maintenance cost is represented by the square of the difference between the phenotypes of neighbouring environmental states, with a cost coefficient k_m. It should be noted that this assumption also has an additional effect on the form of reaction norm (see Results section). In this model, an average phenotypic value $\bar{v}$ is assumed as the constitutive phenotype v_c, which differs from the previous model, which considers an evolvable baseline phenotype as the constitutive phenotype. It should be noted that in this model, the evolution of the baseline phenotype is meaningless. When the cost results from the slope of the reaction norm, the baseline phenotype does not affect the maintenance cost, by which the baseline should be set at the lowest phenotype to minimize the production cost of the constitutive phenotype as long as $k_p < k_c$. To avoid this unrealistic effect, we consider an average phenotype as the constitutive phenotype, which is not evolvable.

To analyse the evolutionarily realized reaction norm, we need to specify a functional form of the state-specific benefit, $f(x, v(x))$. In the following analysis, we assume two types of benefits. The first type of state-specific benefit function is assumed maximized at an intermediate phenotypic value under the given environmental state. The benefit is formulated as:

$$f(x, v(x)) = \alpha - \beta\,(w(x) - v(x))^2, \tag{4}$$

where $w(x)$ represents a beneficial phenotype that maximizes the individual benefit $f(x, v(x))$ as shown in Fig. 1c, for which $w(x)$ increases linearly with x. Following an analysis in Appendix A, we are able to obtain the optimal baseline phenotype v_0* and the evolutionarily realized reaction norm **v***. Another type of benefit function assumes that individual success increases monotonically with increasing phenotypic value. For instance, the phenotypic level of an anti-predator defensive trait may be consistent with this assumption, in which a higher level of defence always results in a larger benefit (it should be noted that this discussion excludes the effect of costs for the phenotype that are denoted separately as equation (2)). In the analysis, we assume a function as follows:

$$f(x, v(x)) = \alpha + \beta x^{\gamma} \log(\varepsilon v(x) + \delta), \tag{5}$$

an example of which is shown in Fig. 1d. Equation (5) is a concave function of $v(x)$ under a fixed environmental state, x. In Appendix A, we derive the optimal baseline phenotype v_0* and the optimum reaction norm **v*** for this $f(x, v)$.

We analyse the evolution of the reaction norm **v** in Models 1 and 2 through approaches that are explained in Appendix A and B, respectively. We assume that environmental states vary with a Gaussian probability distribution within $1 \leq x \leq 100$ ($X = 100$) with a mean value $x = 50$, the standard deviation of which represents environmental variability, σ. Accordingly, $p(x)$ is formulated as:

$$p(x) = \frac{1}{P} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{(x-50)^2}{2\sigma^2}\right], \tag{6}$$

where P is a scaling factor to ensure a total probability of 1 in the interval $1 \leq x \leq 100$.

RESULTS

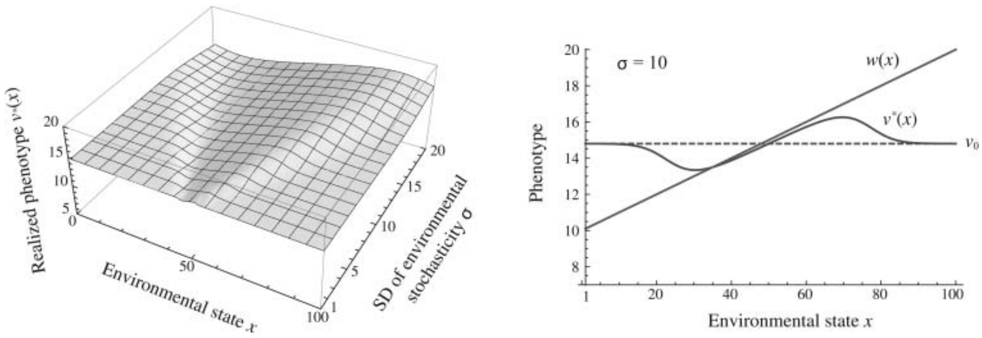
Model 1: Maintenance costs of plasticity resulting from a given amount of flexible response

Case 1: State-specific benefit of a unimodal function of phenotype with a maximum

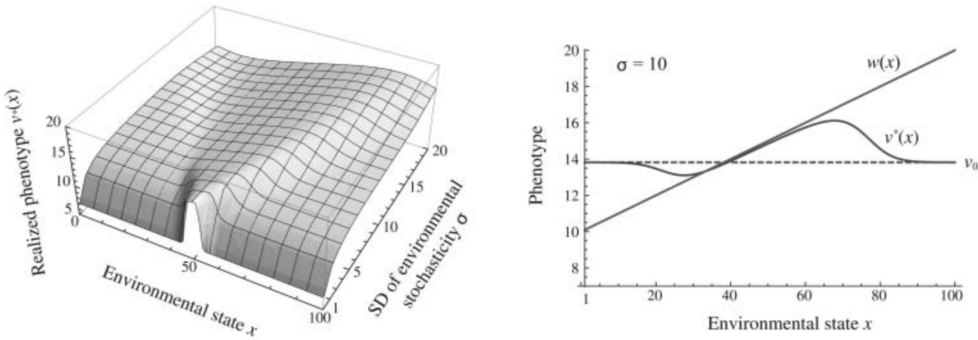
Examples of the evolutionarily realized reaction norm are illustrated in Fig. 2. Figure 2a shows typical patterns of reaction norms when the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$). The right-hand panel of Fig. 2a shows that the reaction norm tends to consist of both downward and upward responses with similar magnitude towards the beneficial phenotype $w(x)$, over the range of common environmental states. This trend does not vary with the maintenance cost of plasticity (k_m). In contrast, Figs. 2b and 2c illustrate reaction norm patterns when the production cost of the plastic response is smaller than that of the constitutive phenotype ($k_p < k_c$), with a small and large maintenance cost of plasticity (k_m), respectively. The right-hand panel of Fig. 2b shows that when the plastic response is less costly than the constitutive phenotype, the organism sets the baseline phenotype at a lower level with a mainly upward response. This is especially apparent at the lowest stochasticity, for which the baseline is very low and the plastic response is entirely upward (left-hand panel of Fig. 2b). However, the right-hand panel of Fig. 2c indicates that the reaction norm is likely to consist of both downward and upward responses with a higher baseline phenotype under a costly maintenance of plasticity except at low environmental variability.

The dependencies of the evolutionarily realized reaction norm on environmental variability are illustrated in the left-hand panels of Fig. 2. To clarify the trend, we propose two indices of plasticity. One index is the amplitude of the reaction norm, which is the difference between maximum and minimum phenotypic values over the whole range of environmental states. The other index is the maximum slope of the reaction norm, which is the maximum of the absolute value of the tangent between phenotypes of neighbouring environmental states. This focuses on a difference of phenotypic values between states, which is an index of the sensitivity of the phenotypic response to a small change in environmental condition. As shown in Fig. 4a, if the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$), the amplitude increases, but the maximum slope decreases with increasing environmental variability (dashed curves). In contrast, when the production cost of the plastic response is smaller than that of the constitutive phenotype ($k_p < k_c$), both indices tend to have strong decreasing trends at low σ (solid curves). The maximum slope decreases more steeply, and the amplitude is likely to be U-shaped with increasing

(a) Benefit function with beneficial phenotype ($k_p = 0.02$, $k_c = 0.02$, $k_m = 0.0001$)



(b) Benefit function with beneficial phenotype ($k_p = 0.01$, $k_c = 0.02$, $k_m = 0.0001$)



(c) Benefit function with beneficial phenotype ($k_p = 0.01$, $k_c = 0.02$, $k_m = 0.001$)

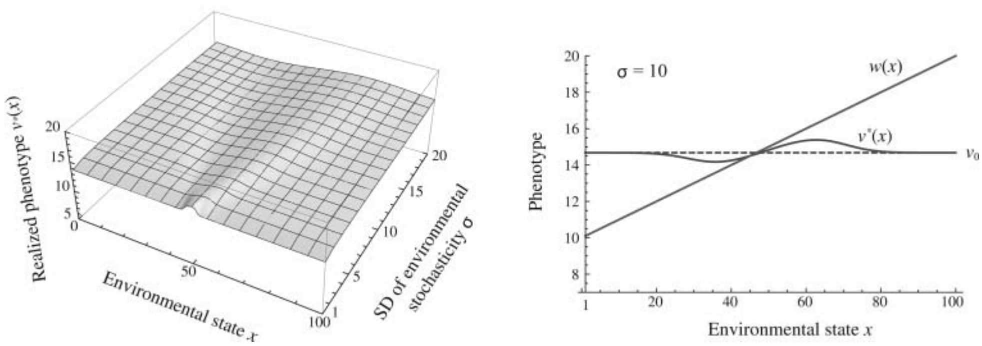


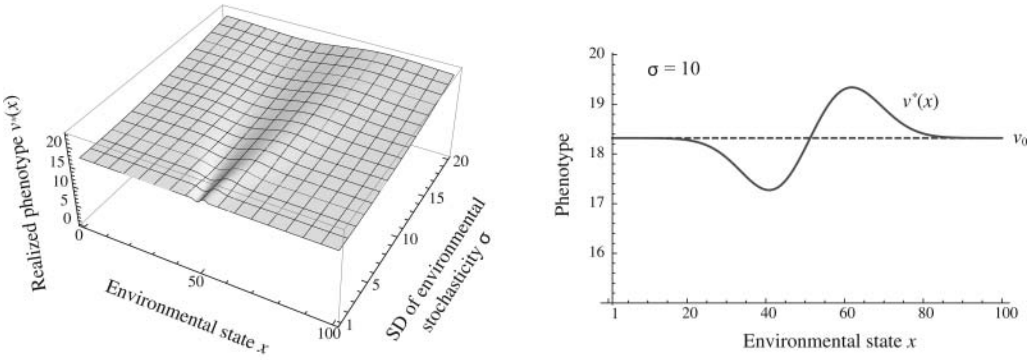
Fig. 2. Examples of the evolutionarily realized reaction norm, $v^*(x)$, when the maintenance cost of plasticity results from a given amount of the plastic response (as in Fig. 1a) and the benefit is maximized at a beneficial phenotype (as in Fig. 1c). The left-hand column illustrates the reaction norm for various levels of environmental variability, σ. The right-hand column is that for $\sigma = 10$ (solid curve) with the beneficial phenotype ($w(x)$: solid line) and the baseline phenotype (v_0: dashed line). In (a), the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$). In (b) and (c), the former is smaller than the latter ($k_p < k_c$), with high and low maintenance costs of plasticity (k_m), respectively.

variability, especially with a small maintenance cost of plasticity (low k_m). The mechanism of this trend is discussed below (see Discussion).

Case 2: State-specific benefit of a monotonically increasing function of phenotype

Examples of the evolutionarily realized reaction norm are shown in Fig. 3. Figure 3a illustrates typical patterns of reaction norms when the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$). In this case, the reaction norm tends to consist of both downward and upward responses with similar magnitude (right-hand panel). On the other hand, Fig. 3b shows the result when the production cost of the plastic response is smaller than that of the constitutive phenotype ($k_p < k_c$), which primarily represents an upward response with a lower baseline phenotype (right-hand

(a) Benefit function increasing with phenotype ($k_p = 0.02$, $k_c = 0.02$, $k_m = 0.0001$)



(b) Benefit function increasing with phenotype ($k_p = 0.01$, $k_c = 0.02$, $k_m = 0.0001$)

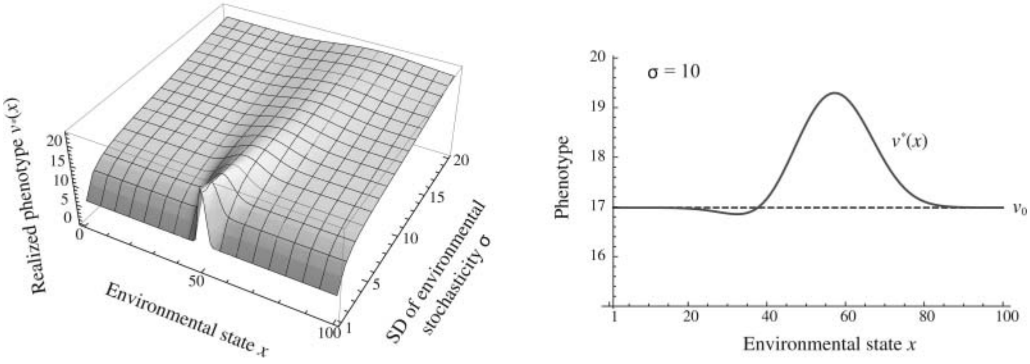
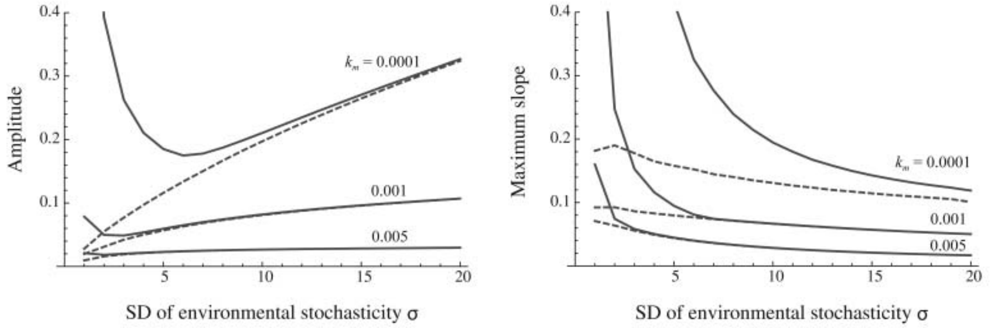


Fig. 3. Examples of the evolutionarily realized reaction norm, $v^*(x)$, when the maintenance cost of plasticity results from a given amount of the plastic response (as in Fig. 1a) and the benefit is a monotonically increasing function of the phenotype (as in Fig. 1d). The left-hand column illustrates the reaction norm for various levels of environmental variability, σ. The right-hand column is that for $\sigma = 10$ (solid curve) with the baseline phenotype (v_0: dashed line). In (a), the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$), whereas in (b), the former is smaller than the latter ($k_p < k_c$).

(a) Benefit function with beneficial phenotype ($k_c = 0.02$)



(b) Benefit function increasing with phenotype ($k_c = 0.02$)

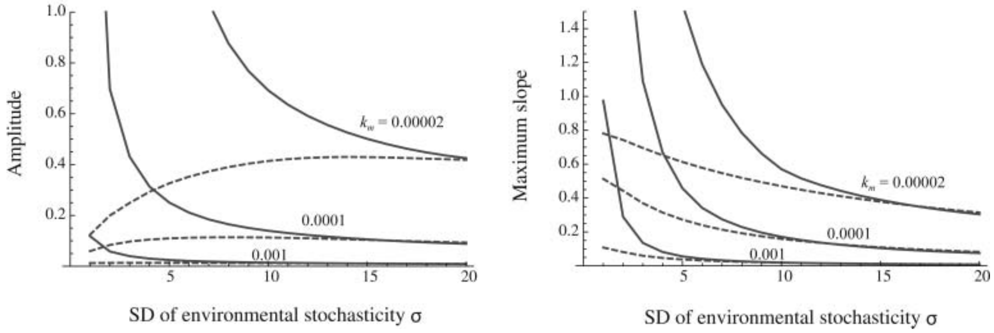


Fig. 4. Two indices of phenotypic plasticity for different levels of environmental variability when the maintenance cost of plasticity results from a given amount of the plastic response (as in Fig. 1a). The left-hand panels are the amplitude of the reaction norm, while the right-hand panels are the maximum slope of the reaction norm. The dashed curves are indices when the production cost of the constitutive phenotype is equal to that of the plastic response ($k_c = k_p = 0.02$), while the solid curves are those when the former is greater than the latter ($k_c > k_p = 0.01$). In (a), the benefit is maximized at a beneficial phenotype (as in Fig. 1c), in which $k_m = 0.0001$, 0.001, and 0.005 from the top to bottom curves for both indices. In (b), the benefit is a monotonically increasing function of the phenotype (as in Fig. 1d), in which $k_m = 0.00002$, 0.0001, and 0.001 from the top to bottom curves for both indices.

panel). This trend is unlikely to be altered by the maintenance cost of plasticity (k_m). In the left-hand panels of Fig. 3, the evolutionarily realized reaction norm is plotted against changing environmental variability. As shown in Fig. 4b, the two indices of the reaction norm indicate some similar trends with the above case 1 (see Fig. 4a). If the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$), the amplitude increases, but the maximum slope decreases with increasing environmental variability (dashed curves). Nevertheless, when the production cost of the plastic response is smaller than that of the constitutive phenotype ($k_p < k_c$), both indices tend to decline with increasing variability (solid curves).

Model 2: Maintenance costs of plasticity resulting from the slope of the reaction norm

Case 1: State-specific benefit of a unimodal function of phenotype with a maximum

Examples of the evolutionarily realized reaction norm are illustrated in Appendix Fig. 1 due to limitations of space. The basic trends in the results are similar to those obtained for case 1 in the above Model 1 (see Fig. 2). If the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$), the reaction norm tends to consist of both downward and upward responses with a similar magnitude towards the beneficial phenotype. When the plastic response is less costly than the constitutive phenotype ($k_p < k_c$), the upward response at frequent environmental states becomes dominant, although such a trend is moderated by an increment in the maintenance cost of plasticity. (Appendix Fig. 1 shows these results in its right-hand panels, and the dependencies of the evolutionarily realized reaction norm on environmental variability in its left-hand panels.)

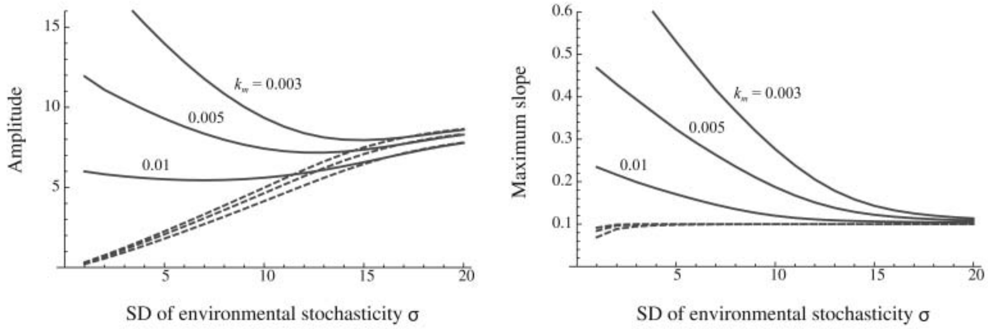
The trend is summarized in Fig. 5a with two indices of plasticity. If the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$), both the amplitude and maximum slope of the reaction norm tend to increase with increasing environmental variability (dashed curves). In contrast, when the production cost of the plastic response is smaller than that of the constitutive phenotype ($k_p < k_c$), both indices involve decreasing trends (solid curves). In this case, the maximum slope decreases, whereas the amplitude is likely to take on a U-shaped form.

Case 2: State-specific benefit of a monotonically increasing function of phenotype

Examples of the evolutionarily realized reaction norm are illustrated in Appendix Fig. 2. The basic trends in the results are similar to those obtained for case 2 in the above Model 1 (see Fig. 3). When the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$), the reaction norm tends to consist of both downward and upward responses of similar magnitude. In contrast, when the production cost of the plastic response is smaller than that of the constitutive phenotype ($k_p < k_c$), an upward response dominates with a lower average phenotype, the tendency of which is not altered by the maintenance cost of plasticity (k_m). (Appendix Fig. 2 shows these results in its right-hand panels, and the dependencies of the evolutionarily realized reaction norm on environmental variability in its left-hand panels.) The trends are summarized in Fig. 5b with two indices of plasticity. If the production cost of the plastic response is equal to that of the constitutive phenotype ($k_p = k_c$), both the amplitude and maximum slope of the reaction norm increase with increasing environmental variability (dashed curves). In contrast, when the production cost of the plastic response is smaller than that of the constitutive phenotype ($k_p < k_c$), the maximum slope shows decreasing trends, but the amplitude continues to increase with increasing environmental variability (solid curves).

In the case of Fig. 5b, the indices show specific characteristics. In other cases (Figs. 4 and 5a), the amplitudes of the reaction norms with $k_p = k_c$ (dotted curve) and $k_p < k_c$ (solid curve) tend to coincide with each other at higher environmental variability. In Fig. 5b, nevertheless, such a coincidence is unlikely to occur, especially with a low maintenance cost

(a) Benefit function with beneficial phenotype ($k_c = 0.02$)



(b) Benefit function increasing with phenotype ($k_c = 0.02$)

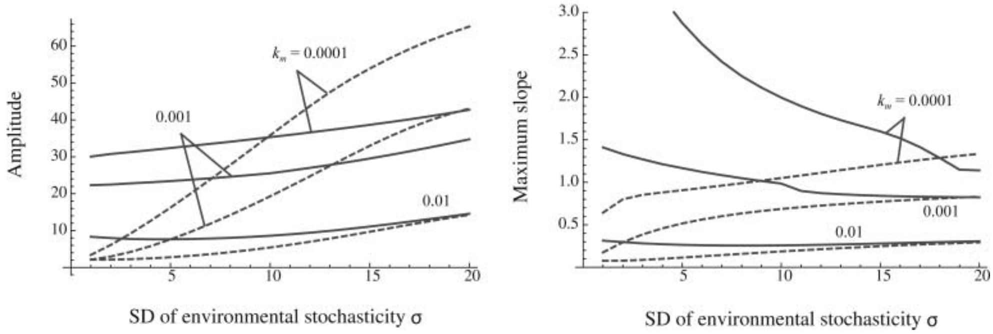


Fig. 5. Two indices of phenotypic plasticity for different levels of environmental variability when the maintenance cost of plasticity results from the slope of the plastic response (as in Fig. 1b). The conditions are similar to those of Fig. 4. The dashed curves are indices with $k_c = k_p = 0.02$, while the solid curves are with $k_c > k_p = 0.01$. In (a) and (b), $k_m = 0.003$, 0.005 and 0.01, and $k_m = 0.0001$, 0.001 and 0.01 respectively.

of plasticity (small k_m). This results from a lower boundary of the phenotypic value, i.e. the value cannot fall below $-\delta/\varepsilon$ based on the benefit function in equation (5). In this model, when the maintenance cost of plasticity is low (small k_m), the reaction norm evolves to reduce the average phenotype, by which the downward plastic response tends to be bounded by the lower limit. This limitation suppresses the amplitude of the reaction norm under $k_p < k_c$, which results in the inconsistency of amplitudes between $k_p = k_c$ and $k_p < k_c$ in highly variable environments (see also left-hand panels of Appendix Fig. 2).

Compared with Model 1 (Figs. 2 and 3), changes in the reaction norm are relatively gradual in Model 2 (Appendix Figs. 1 and 2), especially when there is low environmental variability. This can be explained by the fact that the gradual change can help to minimize the maintenance cost of plasticity in Model 2. However, this is also a functional form of the maintenance cost of Model 2, which is proportional to a sum of squares of the slope of the reaction norm. If the maintenance cost is proportional to a sum of absolute reaction norm slopes (not square), the cost only depends on the endpoints of the reaction norm and not the shape of the curve between them, within a range with a monotonic change of the reaction norm. In such a case, the cost can decrease by reducing the difference between the two endpoints. On the other hand, when the square is included, the cost will be minimized by connecting the two endpoints by a straight line. In both cases, the maintenance cost may make the form of the reaction norm less steep, although the effect would be more significant in the latter case.

In the present analysis, we examined a restricted range of parameters and functions. Despite these limitations, we successfully revealed that the relationships between environmental variability and evolutionarily realized reaction norms could vary depending on the conditions.

Relaxation of some assumptions

In the above analyses, we theoretically studied the evolution of the reaction norm based on some assumptions that may restrict the generality of the results. In order to examine the effects of those assumptions, we conducted additional analyses by modifying the assumptions that the constitutive phenotype is more costly than the plastic response in terms of production (i.e. $k_p \leq k_c$), and that the mode of environmental stochasticity is a spatial fluctuation. Analyses and results are shown in the text and figures in the Appendix, which indicate that the relaxation of model assumptions can also conditionally result in a decreasing trend of indices of plasticity with increasing environmental stochasticity. This suggests that such a trend could be robust for a variety of situations.

DISCUSSION

Observations supporting the evolutionarily realized reaction norm

The analysis performed here results in various forms of reaction norm depending on conditions, which include a unimodal form (e.g. the right-hand panel of Figs. 3b and Appendix Figs. 1b, 1c and 2b), a sigmoidal form (e.g. those shown in Appendix Figs. 1a and 2a), and a form with both downward and upward plastic responses from a constitutive phenotype (e.g. those of Figs. 2a–c). The unimodal and sigmoidal reaction norms have been observed in nature. For example, *Drosophila* exhibited a unimodal response in thorax length to growth temperature, but a sigmoidal response in abdomen pigmentation and egg length (David *et al.*, 2004). In contrast, a reaction norm with both downward and upward plastic responses has rarely been reported. A single report of a diatom species (*Asterionella formosa*) showed a dependence of net production rate on temperature. The rate is relatively flat at low temperatures, decreases at intermediate temperatures, and then increases to high values at high temperatures (Gsell *et al.*, 2013). This may be an example of the reaction norm with both downward and upward plastic responses that occurs at intermediate and high temperatures, respectively.

The present analysis also highlights a relationship between the functional form of the evolutionarily realized reaction norm and the probability distribution of environmental states. According to the analysis, organisms tend to flexibly or constitutively adjust their phenotype for environmental states that frequently occur but ignore those that occur with a low frequency. Hence, if the environmental state follows a Gaussian distribution, as in the present study, such substantial adaptation to frequent environment states could potentially result in a unimodal form of individual success within a range of environmental states. In self-fertilizing nematodes, lifetime fecundity appears to exhibit such a unimodal form in response to temperature (Prasad *et al.*, 2011). Of particular note, the fecundity curve was slightly skewed towards higher temperatures in a tropical strain but towards lower temperatures in a temperate strain, suggesting that the nematodes were likely to cede the ability to respond to relatively rare environmental states in their habitat. This observation supports the expectation of the present analysis that an evolutionarily realized reaction norm may have costs accompanying phenotypic plasticity.

Costs with respect to phenotype

In the present analysis, we consider that costs of phenotype and plasticity can be determinant factors of the reaction norm. In other words, the costs can be important constraints in the evolution of the reaction norm. A meta-analysis of forms of reaction norm indicated that higher-order shapes of the reaction norm are more evolutionarily variable than simpler aspects, i.e. curvature > slope > mean (Murren *et al.*, 2014). This suggests that lower-order shapes of the phenotype are more strongly constrained by accompanying costs, implying the importance of costs in the evolution of reaction norms.

In particular, the maintenance cost of plasticity can be considered an important factor in the evolution of the reaction norm. However, the maintenance cost has seldom been detected in empirical studies (van Kleunen and Fischer, 2005; Van Buskirk and Steiner, 2009). It was pointed out that a potential bias in evaluation could hamper the detection of costs (Auld *et al.*, 2010). It is also possible that the maintenance cost tends to be lost by natural selection purging genotypes burdened by high costs of plasticity from natural populations (DeWitt *et al.*, 1998; van Kleunen and Fischer, 2007). In either case, the empirical measurements suggested that the maintenance cost of plasticity was small in many cases. According to the present analysis, the small maintenance cost (low k_m) tends to enhance a dependency of indices of phenotypic plasticity on environmental stochasticity (see Figs. 4 and 5). Thus, it is to be expected that especially when the production costs differ between constitutive phenotype and plastic response to some degree ($k_p < k_c$ or $k_p > k_c$), the plasticity may decline significantly with increasing environmental stochasticity.

The present study has indicated that costs of phenotypic plasticity are important factors in the evolution of reaction norms, although their direct measurement is quite difficult in nature. However, our approach may contribute to the indirect estimation of the costs accompanying a phenotype (see Appendix).

Negative correlation between environmental variability and phenotypic plasticity

The present study has shown that variability in the environmental state does not necessarily promote the evolution of phenotypic plasticity. We proposed two types of indices for the magnitude of phenotypic plasticity, i.e. amplitude and the maximum slope of the reaction norm. The former indicates variability of the phenotype, whereas the latter corresponds to a sensitivity of the phenotype to a small change in environmental conditions. Our analyses demonstrate that both indices often decline in a strongly varying environment. Key factors of this trend are costs accompanying the phenotype.

The negative correlation between environmental variability and phenotypic plasticity is likely to be significant when the cost coefficient of the maintenance of plasticity is relatively low (small k_m in Figs. 4 and 5) and the constitutive phenotype is more costly compared with the plastic response in production ($k_p < k_c$; solid curves in Figs. 4 and 5). With $k_p < k_c$ and small k_m, a constitutive phenotype would be set at a small value to reduce its production cost. In this situation, if the environment is relatively less variable, phenotypic plasticity is only expressed for frequent environmental states that are very close to $x = 50$ for low variability (see the left-hand panels of Figs. 2 and 3, and Appendix Figs. 1 and 2). With a relatively variable environment, however, the organism has to adapt to a wide range of environmental states. If this is achieved by a plastic response over a wide range of states, the accompanying maintenance cost of plasticity must be substantial despite the low cost coefficient. Therefore, organisms have to set a relatively high constitutive phenotype, thus reducing the plastic responses. This mechanism produces a strong negative correlation between environmental variability and phenotypic plasticity.

The negative correlation between environmental variability and phenotypic plasticity was unexpected, because phenotypic plasticity is considered to be a strategy for enhancing individual success in varying environmental states where the beneficial phenotype notably changes within the range of possible states. However, in a substantially varying environment, the increasing maintenance cost of plasticity cancels the advantage of plasticity. It is remarkable that the costs of plasticity do not only suppress plasticity directly, but also influence the relationship between phenotypic plasticity and environmental stochasticity. Consequently, the balance between the benefits and costs accompanying the phenotype determines the correlation between phenotypic plasticity and environmental stochasticity.

Ernande and Dieckmann (2004) analysed the evolution of the reaction norm using a similar approach to the present model, although their model did not involve a factor that was critical for the results of the present study, i.e. a difference between the production costs of the constitutive phenotype and plasticity. They did not examine the relationship between environmental variability and phenotypic plasticity. However, even if their model had examined this relationship, it would not have been able to elucidate the properties of phenotypic plasticity that were illustrated in the present analysis, due to the absence of this critical factor.

In Model 1, with maintenance costs of plasticity resulting from the amount of flexible response, the reaction norm tends to have a sharp peak around the most frequent environmental state, especially when environmental variability is low (Figs. 2 and 3). This trend, however, may become weak if other factors exist, e.g. error in sensing the environmental condition and developmental instability in expressing the plastic response. The error and instability could result in a mismatch between phenotype and environmental states, which may notably reduce individual success under a steep reaction norm. Accordingly, the reaction norm could be somewhat flat in the presence of those factors, which may modify the relationship between environmental variability and indices of phenotypic plasticity (especially in the right-hand panels of Fig. 4).

Implications of the results

According to the present analysis, the suppression of plasticity by environmental variability is likely to occur when the maintenance cost of plasticity is relatively small (low k_m) and the production cost of the constitutive phenotype is larger than that of the plastic response ($k_p < k_c$). The value of k_p/k_c tends to be small if there is a long time lag between the development of the constitutive phenotype and the plastic response. If the constitutive phenotype develops and establishes at an early stage of life, young individuals may have to pay a relatively high cost for it, due to the relatively brief period available to reserve resources. In addition, they would have to keep the constitutive phenotype over a long period, which involves a cost for maintenance. Therefore, the value of k_p/k_c tends to be small with a substantial time lag between the expression of the constitutive phenotype and the expression of the plastic response, by which the phenotypic plasticity is likely to be significantly negatively correlated with environmental variability.

Our analysis also indicates that an index of phenotypic plasticity should be carefully determined to evaluate the magnitude of phenotypic plasticity. In this study, we proposed two different indices, the amplitude and the maximum slope of the reaction norm, as indicators of the variability of the phenotype and the sensitivity of the response to environmental change, respectively. These indices can exhibit different trends under environmental variability, which could cause inconsistent relationships between phenotypic plasticity and determining factors (e.g. the cost and benefit functions of phenotypic plasticity and the coefficients of costs). To fully examine the effects of these factors on phenotypic plasticity, we need to carefully define and choose the appropriate index for any measurement of phenotypic plasticity.

ACKNOWLEDGEMENTS

We thank the members of the Centre for Ecological Research for their comments and encouragement. This research was supported financially by the Global COE Program A06 at Kyoto University, JSPS Core-to-Core Program Number 20004, and JSPS KAKENHI Grant Numbers 23570023 to A.Y.

REFERENCES

Agrawal, A.A. 2001. Ecology: phenotypic plasticity in the interactions and evolution of species. *Science*, **294** (5541): 321–326.

Auld, J.R., Agrawal, A.A. and Relyea, R.A. 2010. Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proc. R. Soc. Lond. B*, **277**: 503–511.

Berrigan, D. and Scheiner, S.M. 2004. Modeling the evolution of phenotypic plasticity. In *Phenotypic Plasticity: Functional and Conceptual Approaches* (T.J. DeWitt and S.M. Scheiner, eds.), pp. 82–97. Oxford: Oxford University Press.

David, J.R., Gibert, P. and Moreteau, B. 2004. Evolution of reaction norm. In *Phenotypic Plasticity: Functional and Conceptual Approaches* (T.J. DeWitt and S.M. Scheiner, eds.), pp. 50–63. Oxford: Oxford University Press.

DeWitt, T.J., Sih, A. and Wilson, D.S. 1998. Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.*, **13**: 77–81.

Ernande, B. and Dieckmann, U. 2004. The evolution of phenotypic plasticity in spatially structured environments: implications of intraspecific competition, plasticity costs and environmental characteristics. *J. Evol. Biol.*, **17**: 613–628.

Gsell, A.S., Domis, L.N.D., van Donk, E. and Ibelings, B.W. 2013. Temperature alters host genotype-specific susceptibility to chytrid infection. *PLoS One*, **8**: e71737.

Murren, C.J., Maclean, H.J., Diamond, S.E., Steiner, U.K., Heskel, M.A., Handelsman, C.A., Ghalambor, C.K. *et al.* 2014. Evolutionary change in continuous reaction norms. *Am. Nat.*, **183**: 453–467.

Neilson, E.H., Goodger, J.Q.D., Woodrow, I.E. and Moller, B.L. 2013. Plant chemical defense: at what cost? *Trends Plant Sci.*, **18**: 250–258.

Newman, R.A. 1992. Adaptive plasticity in amphibian metamorphosis. *Bioscience*, **42**: 671–678.

Pigliucci, M. 2001. *Phenotpic Plasticity: Beyond Nature and Nurture*. Baltimore, MD: Johns Hopkins University Press.

Prasad, A., Croydon-Sugarman, M.J.F., Murray, R.L. and Cutter, A.D. 2011. Temperature-dependent fecundity associates with latitude in *Caenorhabditis briggsae. Evolution*, **65**: 52–63.

Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.*, **24**: 35–68.

Scheiner, S.M., Barfield, M. and Holt, R.D. 2012. The genetics of phenotypic plasticity. XI. Joint evolution of plasticity and dispersal rate. *Ecol. Evol.*, **2**: 2027–2039.

Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience*, **39**: 436–445.

Thompson, J.D. 1991. Phenotypic plasticity as a component of evolutionary change. *Trends Ecol. Evol.*, **6**: 246–249.

Van Buskirk, J. and Steiner, U.K. 2009. The fitness costs of developmental canalization and plasticity. *J. Evol. Biol.*, **22**: 852–860.

van Kleunen, M. and Fischer, M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytol.*, **166**: 49–60.

van Kleunen, M. and Fischer, M. 2007. Progress in the detection of costs of phenotypic plasticity in plants. *New Phytol.*, **176**: 727–730.

van Tienderen, P.H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution*, **45**: 1317–1331.

van Tienderen, P.H. 1997. Generalists, specialists, and the evolution of phenotypic plasticity in sympatric populations of distinct species. *Evolution*, **51**: 1372–1380.