The timescale of environmental fluctuations determines the competitive advantages of phenotypic plasticity and rapid evolution

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Abstract
Organisms can respond to fluctuating environments by phenotypic plasticity and rapid evolution, both occurring on similar timescales to the environmental fluctuations. Because each adaptation mechanism has been independently studied, the effects of different adaptation mechanisms on ecological dynamics are not well understood. Here, using mathematical modeling, we compared the advantages of phenotypic plasticity and rapid evolution under conditions where the environment fluctuated between two states on various timescales. The results indicate that the advantages of phenotypic plasticity under environmental fluctuations on different timescales depend on the cost and the speed of plasticity. Both the speed of plastic adaptation and the cost of plasticity affect competition results, while the quantitative effects of them vary depending on the timescales. When the environment fluctuates on short timescales, the two populations with evolution and plasticity coexist, although the population with evolution is dominant. On moderate timescales, the two populations also coexist; however, the population with plasticity becomes dominant. On long timescales, whether the population with phenotypic plasticity or evolution is more advantageous depended on the cost of plasticity. Moreover, our results indicate that the mechanisms resulting in the dominance of the plastic population over the population with evolution are different depending on the timescales of environmental fluctuations. Therefore, the timescales of environmental fluctuations deserve more attention if we are to better understand the detailed competition results underlying phenotypic variation.

KEYWORDS
adaptation strategies, environmental fluctuations, evolution, phenotypic plasticity, population dynamics
INTRODUCTION

Environmental fluctuations caused by biotic and abiotic factors occur on various timescales, and organisms exposed to such environmental fluctuations may improve their fitness by modifying their traits. The adaptive mechanisms underlying changes in traits are categorized into two types. The first is the phenotypic adjustment of individual organisms to their environments, and includes phenomena such as phenotypic plasticity and learning. The second is adaptive evolution, driven by natural selection on genetic variation (Shimada, Ishii, & Shibao, 2010). These adaptive mechanisms have ecological consequences on population and community dynamics (Bolnick et al., 2011; Johnson & Stinchcombe, 2007; Miner, Sultans, Morgan, Padilla, & Relyea, 2005).

Phenotypic plasticity, which is the ability to express multiple phenotypes from a single genotype, depending on the environmental conditions, is widespread in nature (Agrawal, 2001; Miner et al., 2005). Plastic organisms can change their traits rapidly without the need for genetic changes over generations. Thus, phenotypic plasticity is an effective way to withstand temporal environmental change. Previous studies have suggested that a trait with phenotypic plasticity is advantageous over a trait after environmental change when environmental conditions fluctuate in a predictable way (Scheiner, 1993) and that such plasticity does not involve large time delays (Padilla & Adolph, 1996; Stomp et al., 2008).

Evolution is another approach to coping with environmental fluctuations. A population with high levels of genetic variation may exhibit improved performance in response to environmental fluctuations compared with the one with low levels of genetic variation, and the long-term maintenance of multiple genotypes is required for evolution to continue (Meyers & Bull, 2002). However, when timescales of environmental fluctuations are short enough to prevent loss of genetic variation, maintenance mechanisms are not necessary. In fact, rapid evolution, manifested as changes in gene frequencies in a population, can produce adaptive trait changes within timescales of several generations (Harriston, Ellner, Geber, Yoshida, & Fox, 2005; Hendry & Kinnison, 1999; Johnson & Stinchcombe, 2007; Thompson, 1998; Yoshida, Jones, Ellner, Fussmann, & Hairston, 2003).

Both types of adaptation are possible within a species simultaneously, and their relative importance differs among populations. To understand such differences, mechanisms of adaptation should be considered in the same framework (Bolnick et al., 2003; Bolnick, Svanbäck, Araujo, & Persson, 2007). Actually, these different types of adaptation have been shown to exhibit varying effects on ecological stability and persistence in predator-prey systems (Cortez, 2011; Kovach-Orr & Fussmann, 2013). Yamamichi, Yoshida, and Sasaki (2011) demonstrated that in a predator-prey system with environments fluctuating on moderate timescales, organisms with phenotypic plasticity have advantages over those exhibiting genetic variation. An empirical study indicated that rapid evolution and phenotypic plasticity result in distinct effects on the population dynamics of four genetically distinct strains of prey algae (Chlamydomonas reinhardtii) that exhibit varied in their growth rates, existing levels of defense, and inducible defenses (Fischer et al., 2014). From an evolutionary perspective, Svanbäck, Pined-Krch, and Doebeli (2009) demonstrated that whether a predator population gains phenotypic plasticity or splits into two non-plastic specialist groups depends on the stability of the predator-prey dynamics. The individual-based model presented by Svanbäck et al. (2009) assumes a spatial structure, and it does not consider the effect of timescales of exogenous environmental fluctuations, rather it is more concerned with the amplitude of population fluctuations. Although the differences in the effects on population and evolutionary dynamics between rapid evolution and phenotypic plasticity in predator-prey interactions have been reported, their effects on competition have seldom been directly compared. Competition is an important biological interaction that affects species evolution (e.g., competitive exclusion), and it is unclear which type of adaptation is effective in competition. Here, we investigate this issue by comparing individuals that employ phenotypic plasticity with those that exhibit rapid evolution.

In this article, we explore how environmental fluctuation on various timescales affect competition among individuals with different adaptive mechanisms. Phenotypic plasticity results in faster changes in phenotype compared with rapid evolution (Olsson & Eklöv, 2005; Svanbäck & Persson, 2004; Svanbäck & Persson, 2009), because phenotypically, plastic organisms can change their traits within a generation. Variations in the speed of adaptation influence population dynamics (Abrams, Matsuda, & Harada, 1993; Mougi, 2012; Mougi & Iwasa, 2010; Mougi & Iwasa, 2011; Tien & Ellner, 2012; Yamamichi et al., 2011). Differences in the underlying mechanisms and speeds of adaptation between phenotypic plasticity and rapid evolution suggests that the optimal adaptive strategy is dependent on the timescale of environmental fluctuations. Intuitively, plasticity has an advantage compared to rapid evolution on short timescales of environmental fluctuation, because rapid evolution is likely to result in slower responses to new environments than does plasticity. However, Stomp et al. (2008) demonstrated, both experimentally and theoretically, that flexible (plastic) phenotypes have disadvantages over specialists that adapt to only one side of two...
different environments, temporally changing when phenotypic adaptation occurs too late in relation to an environmental fluctuation. Thus, there exists a gap between the intuitive prediction and the actual observations. The relationship between the timescale of environmental fluctuations and adaptive strategies requires more clarification, especially with regard to the wide range of timescales of environmental fluctuations.

Here, we investigated a model based on the Lotka-Volterra competition equation to examine when phenotypic plasticity is advantageous over rapid evolution as an adaptive mechanism in response to environmental fluctuation. We assume evolution as the frequency change of two specialist genotypes (Abrams & Matsuda, 1997; Jones & Ellner, 2007; Yamamichi et al., 2011; Yoshida et al., 2007), and in our model, evolutionary trait change occurs as genotype frequencies changed, and the speed of evolution depends on selection pressure on the genotypes. Changes in the plastic trait are represented in our model by a response over time when an environment fluctuates. In the model, the speed of plasticity is relatively faster than that of evolution, although we do not explicitly set the adaptation speed of evolution. The model essentially has the same framework as a model of one generalist that can flexibly change its traits without selection after environmental change and two specialists. Previous theoretical studies of one-generalist-and-two-specialists systems have predicted that a fluctuating environment allows the coexistence of the generalist and the specialists (Abrams, 2006a, 2006b; Egas, Dieckmann, & Sabelis, 2004; Stomp et al., 2008; Wilson & Yoshimura, 1994); however, these studies have not investigated quantitative effects on the timescale of environmental fluctuations to competition outcomes between populations with different adaptation mechanisms. We focus on how the timescale of environmental fluctuations influences the relative importance of phenotypic plasticity and rapid evolution in competition and the underlying mechanisms.

2 | MODEL

2.1 | Dynamics of the populations with plasticity and evolution

We classify fluctuating environments into two different states that interchange over time. These two conditions are designated condition A and condition B, and they transition discretely from one to the other in the time interval, \( r \). We assume that the time intervals of the two conditions are identical, although relaxing this symmetric assumption did not affect our main conclusion (see Supporting Information text and Figures S1–S3). To compare the advantages of plasticity and rapid evolution, we assume that there are two types of populations, each of which has one of the two modes of adaptation. Evolution occurs with a change in the frequency of two specialist genotypes, where Genotypes 1 and 2 are better suited to conditions A and B, respectively. The population consisting of Genotypes 1 and 2 are allowed to evolve by natural selection, and the mean trait value of the population is determined by the frequency of these two genotypes. The densities of Genotypes 1 and 2 are \( N_1 \) and \( N_2 \), respectively, and the total density of the population with evolution that has genetic variation, \( N_E \), is given by:

\[
N_E = N_1 + N_2. \tag{1}
\]

Plasticity is defined as a flexible phenotype that changes in response to environmental fluctuations. The density of the population with plasticity is \( N_P \), and a proportion of individuals expressing the plastic response in the population with plasticity, \( q \), fluctuated between 0 and 1. When \( q = 1 \), all organisms of the population with plasticity are identical to genotype 1 of the population with evolution, and when \( q = 0 \), all organisms of the population with plasticity are identical to Genotype 2 of the population with evolution. Here, we assume that the populations with plasticity and evolution consists of an asexually reproducing species, and \( N_1 \), \( N_2 \) and \( N_P \) are densities of different genotypes (clones). The proportion, \( q \), of the population with plasticity changed at a speed of \( \alpha \), when it is exposed to a new environment; however, this plasticity is associated with the costs described below. When the population with plasticity is exposed to a new environment of condition A, the trait changed as:

\[
\frac{dq}{dt} = \begin{cases} \alpha & \text{if } q < 1 \\ 0 & \text{if } q = 1 \end{cases}. \tag{2}
\]

We adopted a simple linear response here, but we also analyzed a sigmoid function as a non-linear response (see Supporting Information text and Figure S4). The proportion, \( q \), of the plastic population approaches, and either reaches or does not reach 1, dependent on the speed of the plastic changes. Similarly, in condition B, the proportion of the adaptive individuals changes toward 0 at a speed of \( \alpha \), thus, \( q \) is given by:

\[
\frac{dq}{dt} = \begin{cases} -\alpha & \text{if } q < 1 \\ 0 & \text{if } q = 1 \end{cases}. \tag{3}
\]

We constructed a competition model under fluctuating environments by expanding the Lotka-Volterra
competition equations. The dynamics of population $N_i (i = 1, 2, P)$, are given by:

$$\frac{dN_1}{dt} = (r_1 - \beta_{i1} N_1 - \beta_{i2} N_2 - \beta_{iP} N_P)N_1,$$  \hspace{0.5cm} (4a)

$$\frac{dN_2}{dt} = (r_2 - \beta_{21} N_1 - \beta_{22} N_2 - \beta_{2P} N_P)N_2,$$  \hspace{0.5cm} (4b)

$$\frac{dN_P}{dt} = (r_P - \beta_{P1} N_1 - \beta_{P2} N_2 - \beta_{PP} N_P)N_P,$$  \hspace{0.5cm} (4c)

where, $r_i (i = 1, 2, P)$ is the intrinsic growth rate and $\beta_{ij} (i, j = 1, 2, P)$ describes the interaction effects from the population $j$ to $i$. The intrinsic growth rate and the interaction effects for the population with plasticity are determined by how close the trait of the population with plasticity is to that of the specialist genotypes, depending on the proportion, $q$. Thus, they are given by:

$$r_p = (q r_1 + (1-q) r_2)(1-c),$$  \hspace{0.5cm} (5a)

$$\beta_{1P} = q \beta_{11} + (1-q) \beta_{12},$$  \hspace{0.5cm} (5b)

$$\beta_{2P} = q \beta_{21} + (1-q) \beta_{22},$$  \hspace{0.5cm} (5c)

$$\beta_{P1} = q \beta_{11} + (1-q) \beta_{21},$$  \hspace{0.5cm} (5d)

$$\beta_{P2} = q \beta_{12} + (1-q) \beta_{22},$$  \hspace{0.5cm} (5e)

where, $c (0 \leq c < 1)$ is the cost of plasticity. We assume the cost of plasticity as a reduction of intrinsic growth rate (DeWitt, Sih, & Wilson, 1998), which is independent of the environmental fluctuations and is an important factor as an adaptation of plasticity theoretically (Yamauchi & Takahashi, 2014). Then $\beta_{PP}$ is expressed by a combination of the interactions among the phenotypes behaving like genotype 1 or 2 in the population with plasticity. Thus, it can be given by:

$$\beta_{PP} = q^2 \beta_{11} + q(1-q)(\beta_{12} + \beta_{21}) + (1-q)^2 \beta_{22}. \hspace{0.5cm} (6)$$

Next, we set carrying capacities as $K_1 = r_1/\beta_{11}$, $K_2 = r_2/\beta_{22}$, and $K_P = r_P/\beta_{PP}$. We consider competition coefficients as $\gamma_{12} = \beta_{12}/\beta_{11} = \beta_{12}/\beta_{22}$ and $\gamma_{21} = \beta_{21}/\beta_{11} = \beta_{21}/\beta_{22}$ by assuming $\beta_{12} = \beta_{22}$. This assumption implies that the interactions among the same genotype are identical. From above, we obtain the model with a style of the Lotka-Volterra competition equations as:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1 + \gamma_{12} N_2 + (q + (1-q) \gamma_{12}) N_P}{K_1}\right), \hspace{0.5cm} (7a)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_1 + N_2 + (q \gamma_{21} + 1-q) N_P}{K_2}\right), \hspace{0.5cm} (7b)$$

$$\frac{dN_P}{dt} = (q r_1 + (1-q) r_2)(1-c)N_P$$

$$\times \left(1 - \frac{(q + (1-q) \gamma_{21}) N_1 + (q \gamma_{21} + 1-q) N_2 + Q N_P}{(qK_2 + (1-q)K_2)(1-c)}\right), \hspace{0.5cm} (7c)$$

where, in short, we set $Q = q^2 + (1-q)^2 + q(1-q)$ ($\gamma_{12} + \gamma_{21}$).

### 2.2 Model parameters

To consider the environmental change, we set different parameter values for the carrying capacities depending on the conditions. Here, we call $K(i=1, 2)$ in condition A as $K_{iA}$ and that in condition B as $K_{iB}$. We set $K_{iA} > K_{2A}$ and $K_{2B} > K_{1B}$ as genotype 1 or the population with plasticity with $q = 1$ fits to condition A; and genotype 2 or the population with plasticity with $q = 0$ fits to condition B. A symmetric competitive situation between conditions A and B was assumed, and we therefore set $\gamma_{12} = \gamma_{21} = \gamma$, $K_{1A} = K_{2B}$, and $K_{2A} = K_{1B}$. Other than these symmetric assumptions, we investigated asymmetric conditions. The results were qualitatively different; however, the difference was explained by the same mechanisms as in symmetric conditions (see Supporting Information text and Figures S1–S3). We assume identical growth rates, such that $r_{1A} = r_{2A} = r_{1B} = r_{2B} = 1$. We define $r$ as the reference value to compare among the timescales of adaptation speed of plasticity, environmental change and growth speed. As plastic organisms cannot adapt effectively when phenotypic plasticity occurs too slowly (Stomp et al., 2008), we set the speed of plasticity, $\alpha = 1$ and the timescale of environmental change, $\tau \geq 1$. $\alpha = 1$ indicated that the plastic trait changes linearly from one extreme trait to the other in one unit of time. Plastic changes are usually faster than evolutionary trait changes (see Section 3). When we set $\alpha = .1$ and .01, speed of adaptation decreases in spite of the constant growth speed. The values and descriptions of the parameters are provided in Table 1.

Numerical simulations of the model were performed with a fourth-order Runge–Kutta procedure for time integration using C++, and the results were checked using Mathematica 9.0.1 (Wolfram Research 2013). In the
numerical simulation, we set the extinction threshold, $\delta$, as $10^{-3}$, so that a population becomes extinct if their number decreased to below $10^{-3}$.

### 2.3 Evaluating the dominant adaptation strategy

We introduce the index, $V_t$, which was defined as:

$$V_t = \int_{t}^{t+2\tau} \frac{N_E}{N_P + N_E} dt,$$

where $t$ was large enough that $(V_t + 2\tau - V_t)/2\tau < 0.001$. This index assesses the relative abundance of the populations with plasticity and evolution for one cycle period of condition $A$ or $B$. $V_t < 0.5$ indicates that plasticity is dominant, whereas a $V_t > 0.5$ indicates that evolution is dominant. Rather than the rate of competitive exclusion, which has previously been used to assess competitive advantage (Grover, 1988; Passarge, Hol, Escher, & Huisman, 2006; Stomp et al., 2008), we use the above index to determine the relative importance of the two adaptation strategies in the case of coexistence.

### 3 RESULTS

#### 3.1 Competition and coexistence of plasticity and rapid evolution

The competition and coexistence of plasticity and rapid evolution are dependent on the timescale of environmental fluctuations, the competitive coefficient, and the cost of plasticity (Figure 1). The advantage of plasticity increases with increasing competitive coefficient $\gamma$ and decreasing cost of plasticity. Coexistence is predicted to be more likely with an intermediate competitive coefficient ($\gamma = 0.75$). The population with evolution exhibits advantages over the population with plasticity when the competitive coefficient is low. At a high cost of plasticity, environmental fluctuations across long timescales also increase the competitive advantage of the population with evolution. With competitive coefficients of $\gamma = 0.60$ or 0.75 and very fast environmental changes, the populations with evolution and plasticity tended to coexist. However, when the environment changes slowly, the coexistence of the populations with evolution and plasticity is predicted under limited circumstances. Moreover, there appears to be an anomalous boundary when the competitive coefficient is intermediate ($\gamma = 0.75$) (Figure 1b, white arrow).

![Figure 1](image)

**Figure 1** Phase diagram of the advantage of adaptation strategies. (a) $\gamma = 0.60$; (b) $\gamma = 0.75$; (c) $\gamma = 0.90$. Black region means existence of only the population with evolution. White region means existence of the population with plasticity. Gray region means coexistence of two populations. White arrow indicates the anomalous boundary. Darker gray indicates relative higher abundance of the population with evolution. The other parameters are the same as those in Table 1.

### TABLE 1 The characteristics of the model parameters

| Parameters | Description | Value |
|------------|-------------|-------|
| $K_{1A}$   | Carrying capacity of Genotype 1 in Condition $A$ | 100   |
| $K_{2B}$   | Carrying capacity of Genotype 2 in Condition $B$ | 100   |
| $K_{1B}$   | Carrying capacity of Genotype 1 in Condition $B$ | 70    |
| $K_{2A}$   | Carrying capacity of Genotype 2 in Condition $A$ | 70    |
| $r$        | Intrinsic growth rate | 1     |
| $\alpha$   | Speed of plastic change | 1     |
| $\gamma$   | Competition coefficient | Variable |
| $c$        | Cost of plasticity | Variable |
| $N_1(0)$   | Initial density of Genotype 1 | 1     |
| $N_2(0)$   | Initial density of Genotype 2 | 1     |
| $N_P(0)$   | Initial density of plastic organism | 2     |
Regarding population and traits dynamics (the temporal change in $q$ and the genetic frequency of population with evolution), we find that changes in the timescales of environmental fluctuations result in four different patterns (Figure 2). The following patterns appear as the timescales of environmental fluctuations increase. First, the population with evolution rapidly achieves and maintains a dominance over the population with plasticity ($V_t = 0.76$), and their abundances remains almost constant (Figure 2a); in this case, the population with plasticity largely changes its trait, while the population with evolution exhibits less trait alteration (Figure 2b). Second, the population with plasticity is dominant ($V_t = 0.34$), and the population abundances oscillate moderately (Figure 2c); where this is case, the population with plasticity adapts to the new environment in a shorter time than the population with evolution, and the population with evolution cannot fully adapt to the new environments (Figure 2d). Third, the population with evolution becomes dominant ($V_t = 0.67$), even though the population with plasticity is more abundant for a short period of time, and the population abundances underwent large amplitude oscillations (Figure 2e); here, the population with evolution is able to fully adapt to the new environments (Figure 2f). Finally, the population with plasticity is more abundant over a cycle period ($V_t = 0.40$), and population abundances exhibits the largest amplitude oscillations (Figure 2g). In the last pattern, one specialist genotype ($N_2$) becomes extinct during the first cycle, and thus, the trait of the population with evolution is fixed and they can no longer adapt by natural selection (Figure 2h).

### 3.2 The effects of the speed of plasticity

We next changed parameter $\alpha$, to investigate how the speed of phenotypic plasticity affected the outcomes of competition between population with plasticity and evolution. When the speed of phenotypic plasticity is lowered from 1 to 0.1 and 0.01, the advantage of the population with phenotypic plasticity diminished to some extent (Figure 3). The population with evolution is advantageous when the environment changes over short timescales (Figure 3a), while this advantage is not observed when the speed of phenotypic plasticity is fast ($\alpha = 1$, Figure 1b). This advantage of the population with evolution increases with decreasing $\alpha$ (Figure 3b).
advantage persists even when $c = 0$, implying that the population with plasticity is at a disadvantage when the adaptation speed of plasticity is slow relative to the speed of environmental change.

4 | DISCUSSION

The results of our analysis of competition between populations exhibiting phenotypic plasticity and rapid evolution suggest that the relative importance of the two adaptation strategies strongly depends on the timescale of environmental fluctuations. Decreasing the competitive coefficient, $\gamma$, decreases the advantages of the population with plasticity, and the coexistence of two adaptive strategies is more likely to occur when the competitive coefficient is intermediate (Figure 1). In our model, low competitive coefficients benefit the population with evolution. When the competitive coefficient is low, reduction of maladapted genotype in population with evolution is small, which leads to fast adaptation in the next new environment because the abundance of the genotype can be more secured from the beginning of the new environment; hence, decreasing the competitive coefficient is their advantage over the population with plasticity. When the competitive coefficient is high, the population with plasticity that has already adapted to a new environment excludes the population with evolution that has not yet adapted to the new environment because the frequency of maladapted genotype in the population with evolution decreases more and the increase of the genotype in the next new environment is delayed.

In an intermediate competitive coefficient ($\gamma = 0.75$, Figure 1b), with short timescales of environmental fluctuations (e.g., $\tau = 2$), the two populations with adaptive strategies coexist (Figure 1), although the population with evolution that consisted of two specialist genotypes dominates (Figure 2a). With rapid environmental change, the specialist genotypes in the maladapted environment avoid drastic decreases in their density. As a consequence, the specialist genotypes maintain their populations, and the trait of the population with evolution only slightly changes (Figure 2b). When these dynamics occur, the relative abundance of the population with plasticity remains low because when the environment switches, almost half of the population with evolution represent adaptive genotypes and the population with evolution rapidly adapts to the new environment, while the flexible generalists require an induction time during which they exhibit plastic trait change. Because this pattern occurs even when $c = 0$, the advantage for the population with evolution on short timescales arises due to a delay of adaptation by the phenotypic plasticity.

On moderate timescales of environmental fluctuations (e.g., $\tau = 20$) that are long enough to reduce specialist genotypes sufficiently in unfavorable environments, the population with plasticity is dominant to the population with evolution (Figure 2c). In this case, the cost of plasticity determines whether the two adaptation strategies coexist, or only the population with plasticity is sustained. On these timescales, the traits of the population with evolution exhibit larger amplitude oscillations than they do on shorter timescales (Figure 2d). This results in the population with plasticity benefiting more from the fitted environment, while specialist genotypes that experienced the maladaptive environment take a long time to recover their density after the environmental change. Therefore, the relative abundance of the population with plasticity increases when the timescales of environmental fluctuations increase from short to moderate.

During long timescales of environmental fluctuations (e.g., $\tau = 80$), the population with evolution is dominant (Figure 2e). As the timescales are sufficiently long for the population with evolution to recover their density, they eventually adapt more effectively than do the population with plasticity because of the cost of plasticity, even though the population with plasticity is better adapted to the environment immediately after the environmental change (Figure 2f). This results in a convex-upward relationship between the advantage of plasticity and the timescale of environmental fluctuations (Figure 1). However, if the cost of plasticity is sufficiently low, this convex-upward relationship never occurs, and the relative abundance of the population with plasticity monotonically increases as the timescale of environmental fluctuations increases (Figure 1). This indicates that the cost of plasticity is critically related to the advantage of the population with evolution on longer timescales of
environmental fluctuations while it does not strongly affect their advantage during short timescales.

When the timescales of environmental fluctuations are much longer (e.g., $\tau = 150$) and one specialist type of the population with evolution tends toward extinction (Figure 2h), the relative abundance of the population with plasticity again increases. This discontinuous change results from the loss of genetic diversity in the population with evolution. Our model demonstrates that this change in relative abundance depends on the assumption of the mechanism of genetic diversity maintenance in the population with evolution. Hence, the maintenance of genetic diversity has a positive effect on the population with evolution, which allows their traits to change through natural selection.

The speed of plasticity also affects the relative importance of the two adaptive strategies. When the speed of plastic adaptation is slow, the relative abundance of the population with plasticity drops overall (Figure 3). Stomp et al. (2008) showed that the plastic generalist genotype is dominant to specialist genotypes when the plasticity has sufficient time to fully adjust to its environment. In this case, the speed of plastic adaptation is relatively slower than the speed of environmental change, and the speed of plastic adaptation affects the results of competition between the generalist genotype and the specialist ones. This result corresponds to the observed increase of plasticity from the short to the moderate timescales of fluctuating environments in our model. On short timescales, the population with evolution has an advantage, even when the cost of plasticity is low. This indicates that the patterns are not driven by the cost of plasticity but rather by the time lag in plastic adaptation. Furthermore, we also analyzed a case with a sigmoid response of the plastic trait change. In this case, the population with evolution benefits, for the most part (Figure S4), as the sigmoid response of the plasticity hampers fast responses from the previously adapted one. Thus, the response speed of plasticity is an important factor in the competition, independent of the cost of plasticity.

In this study, we assumed a reduction of intrinsic growth rate as the cost of plasticity, while the time lag of plastic adaptation is also regarded as a cost of plasticity (DeWitt et al., 1998). Our results suggest that the time lag of plastic adaptation is important from short to moderate timescales, whereas the cost of plasticity is important on long timescales. The appearance of different costs depending on timescales may partly explain why it is difficult to detect the same costs of plasticity in different experiments and field surveys that operate on variable timescales (Auld, Agrawal, & Relyea, 2010). Organisms with long life spans might have slower growth speed than those with short life spans. Thus, the timescale of environmental change that organisms with long life spans experience is relatively shorter than in the case of short life spans. Thus, the speed of plastic adaptation might be important for organisms with long life spans, while the cost of plasticity might be significant for those with short life spans.

As we focused on a comparison of different adaptation mechanisms, we do not explore the evolution of plasticity in our model, although plasticity itself is an evolvable trait (Abrams et al., 1993; Price, Qvarnström, & Irwin, 2003; Shimada et al., 2010; Svanbäck & Persson, 2009). A previous study reported that the cost of plasticity is an important factor in determining whether phenotypic plasticity can evolve in a predator–prey system (Svanbäck et al., 2009). Our results also suggest that the cost of plasticity may affect its evolution, as the cost influences whether the plastic generalist genotype out-competes the specialist genotypes during environmental fluctuations from moderate to long timescales (Figure 1b). By contrast, Svanbäck et al. (2009) reported that the speed of plastic change does not affect the evolution of plasticity. In our model, higher speeds of plasticity also promote its advantage to some extent (Figure 3), although the effect appears to be smaller than that of the cost of plasticity. Therefore, our results are qualitatively similar to those of Svanbäck et al. (2009) with some differences, although the model formulations differ in the two studies.

In this study, we assumed that the populations with plasticity and evolution consists of an asexually reproducing species, and different genotypes (clones) with distinct traits compete with each other. Although clonal dynamics models can reproduce well the actual observed dynamics such as in small green algae (Kasada, Yamamich, & Yoshida, 2014; Meyer, Ellner, Hairston Jr, Jones, & Yoshida, 2006), these models are quite different from those for sexually reproducing species. Two different effects of sexual reproduction can be considered in the context relevant to this study. The maintenance of genetic variations within a population with evolution by sexual reproduction may make the evolutionary response to a new environment faster. On the other hand, producing specialist genotypes with intermediate traits by sexual reproduction might result in maladaptation (i.e., outbreeding depression) or improved adaptation (i.e., hybrid vigor). Thus, the relationship between the timescale of environmental fluctuations and adaptive strategies deserves to be studied in future. An individual-based model that explicitly assumes sexual reproduction and adaptation strategies is surely a candidate.

In conclusion, the advantage of the population with plasticity changes depending on the timescales over which they occur. Changes in population dynamics and the advantages of different adaptive mechanisms over a range of timescales of environmental fluctuations depend on the cost and the speed of plasticity and the intensity of
competition. In addition, the results indicate that the mechanisms that result in the dominance of the population with plasticity over the population with evolution are different depending on the timescales of the environmental fluctuations. On short timescales, the speed of plastic adaptation is important, while the cost of plasticity is a critical factor on long timescales. More attention should be paid to the timescales of environmental fluctuations to facilitate better understanding of the mechanisms underlying phenotypic variation.

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Additional supporting information may be found online in the Supporting Information section at the end of this article.

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