Plasticity's role in adaptive evolution depends on environmental change components

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1 Introduction

Understanding, quantifying, and predicting the ability of organisms to adapt to changing environments is at the core of eco-evolutionary research[1,2]. In the face of unprecedented environmental change, natural populations, especially those with limited mobility, can avoid extinction via **phenotypic plasticity** and/or **adaptive evolution** [3]. However, our understanding of the interplay between selection and plasticity in changing environments is surprisingly limited[4–8]. This limitation is not trivial, for plasticity can itself evolve[9], can be adaptive or nonadaptive[10], and has seemingly contradictory effects on adaptive evolution[11], on which we focus here. For decades, researchers have theorized whether plasticity facilitates or hinders adaptive evolution[9,12]; the evidence is contradictory and general patterns have not emerged [5,10,11,13,14].

The primary conflicting hypotheses for whether plasticity facilitates or hinders adaptive evolution are:

(H1) plasticity weakens directional selection by masking genotypic variation (**Bogert Effect** [15]), thus slowing the rate of genetic change[5,16–18] vs.

(H2) plasticity facilitates evolution by allowing the population to persist under environmental change long enough for genetic change to occur[19–22] (Plasticity-First Hypothesis [21] orBaldwin Effect [19]).

This debate remains unresolved, for even when theoretical predictions agree with empirical findings[5,10,11,13,14,23], we lack a general framework to ascertain the context-dependency of the prevalent mechanism. Here, we introduce a framework based on environmental change context, to outline clear null hypotheses for when and how plasticity interacts with directional evolution. We place the plasticity facilitates vs. hinders selection debate on two ends of a continuum, and specify the properties of environmental change-**rate of mean change**, **variability**, and**temporal autocorrelation** –that influence how plasticity impacts adaptive evolution.

The type of environmental change a population experiences can alter its likelihood of adaptation and, ultimately, persistence[24–27]. Studies of demographic[28], genetic[29], and evolutionary rescue[30], show that rate of mean change, variability, and temporal autocorrelation of a population's selective environment impact population persistence[24,25,29,31–35]. However, because different types of environmental change can have contradictory effects on plasticity and evolution[34,36–38], elucidating these dynamics is not trivial. Consequently, there is an urgent need to place this discussion on the environmental stage in a generalizable way that will allow ecologists and evolutionary biologists to better contextualize, mechanistically understand, predict, and compare their findings.

Moving optimum theory links environmental change to the resulting evolutionary responses. Three decades of research on this theory shows that, when a population is confronted with an environment that

changes directionally, there is a **critical rate of change**that must be matched by change in the mean phenotype of the population, such that the mean remains close to the theoretical **phenotypic optimum**. In this context, a **phenotypic lag** between the mean phenotype and the optimum phenotype typically emerges which, if too large, makes extinction certain [39–41]. Evolutionary (*e.g.*, selection, genetic variation) and ecological processes (*e.g.*, within-generation life history, plasticity and population dynamics) together influence the limit of how far a population can lag without going extinct. The contribution of plasticity to population persistence and adaptation is largely determined by this phenotypic lag: how much of the short-or long-term lag can be compensated for or even hindered by plasticity?

We argue that hypotheses such as the Bogert Effect and the Plasticity-First Hypothesis / Baldwin Effect are not mutually exclusive. Rather, plasticity may facilitate or hinder adaptive evolution depending on the properties of environmental change. To assess the impact of plasticity on the ability of a population to evolutionarily track a changing environmental optimum, we specify the links among the type of environmental change, plasticity, and adaptive evolution by considering several fundamental processes. Thus, we utilize both theoretical and experimental studies to:

Assess how three key components of environmental change (*rate of mean change*, *variability*, and *temporal autocorrelation*) each alter the mechanisms behind phenotypic tracking of a moving optimum ([i] *Genetic variation*, *heritability*, and *selection*, and [ii] life history, *plasticity and population dynamics*).

Introduce a unified framework of testable hypotheses detailing how those three components of environmental change can influence the relative benefit of plasticity to adaptive evolution.



Figure 1. Framework to assess the environment-dependent impact of phenotypic plasticity on adaptive evolution. First, the three key environmental change components (rate of change, variance and autocorrelation) each influences the two broad categories of non-plastic mechanisms through which natural populations

respond to changing environments. The first category encompasses evolutionary processes, such as heritability, genetic variation, and natural selection. The second consists of ecological processes such as demographic dynamics driven by fluctuations in population size and life history. At the core of our conceptual framework, all mechanisms discussed influences how well a population tracks the fitness peak, which shifts as the environment changes. Plasticity enters the framework by impacting a populations' ability to adaptively track the fitness peak. Decomposing environmental change into key components in this fashion allows us to contextualize the magnitude and direction of plasticity's impact on population persistence and adaptive evolution, by way of the mechanistic links.

2 Mechanism of evolutionary response to changing environments: genetic variation, heritability, and selection

The genetic architecture of a trait under selection will in part determine the potential for adaptive evolution, as well as the impact of plasticity on adaptive tracking. The rate at which a trait responds to selection is determined by the number of genes that affect the trait, and the magnitude of their impact. Traits determined by many genes of small effect can respond rapidly if most of the loci are variable at intermediate frequencies [42–44]. To understand plasticity's role in adaptive evolution, we first need to consider how different environmental changes impact the mechanisms of evolutionary tracking in the absence of plasticity. For adaptive evolution to occur, natural selection must act on variation in a heritable trait that affects fitness. Most traits that mediate population dynamics are determined by many genes each of which has small effects: they are quantitative traits, not Mendelian, traits. One way to assess whether or not a quantitative trait may evolve is with the breeder's equation, which states that the change in a trait equals the selection differential multiplied by its narrow-sense heritability. Heritability is a function of both genetic variation [45,46] and the environment in which that variation is expressed [47]. The contributions of environmental change/variation to phenotypic and genetic variation are often relegated to an error term that absorbs unmeasured uncertainties in quantitative genetic models ([48], but see [49]). By making explicit the ways in which rate of mean change, variability, and temporal autocorrelation in the environment each influence heritability, genetic variation, and selection, we aim to understand the ability of genetic change to track an evolutionary optimum in changing environments, and the role of plastic responses in decreasing phenotypic lag.

Impact of the rate of environmental change on underlying genetics

When the rate of environmental change is too slow, selection is weak and can be ineffective in part due to **lag load** [50–52]. As the rate of environmental change increases, selection strengthens, and the population can track the moving optimum with a consistent phenotypic lag[53]. In this range of environmental change, in some contexts additive genetic variance and heritability can also increase[50,54]. In this case, up to a certain intermediate rate of environmental change, genetic variation and evolutionary potential may be expected to increase simply from an increase in standing variation available to selection. However, phenotypic lag can become too large for the rate of selection to follow if the environment, and thus the optimal trait, changes too quickly[50,53,55]. Here, the gap between the mean trait in the population and the optimal trait increases, which can lead to decreased fitness and eventually extinction[56]. As such, the mean time to extinction in a natural population decreases as the rate of environmental change increases beyond the optimal rate[50].

Studies that directly assess the role of environmental variability and temporal autocorrelation on genetic variation and heritability are limited. However, increasing environmental variability, similar to the rate of change, elicits a maximal response to selection at an intermediate magnitude that optimizes selection and ultimately **evolutionary tracking** [57,58]. In contrast, the ability of populations to evolutionarily track a shifting adaptive peak increases with greater temporal autocorrelation because that implies increased predictability of future environments[41,56]. Moreover, positively autocorrelated environmental fluctuations can increase additive genetic variance[59]. Thus, evolutionary potential may be higher in temporally autocorrelated environments.

Impact of environmental variation and temporal autocorrelation on underlying genetics

Research on the evolutionary effect of environmental variability and autocorrelation is often framed in terms of increasing frequencies of **novel and unfavourable environments** [60]. Greater environmental variability and lower temporal autocorrelation expose individuals to environments that are novel and often unfavourable, and their impact on the evolutionary response is mixed depending on other factors at play. One direct consequence of higher variability and lower autocorrelation is that individuals and populations spend less time in **temporal refugia** [31], which reduces fitness. On the other hand, exposure to unfavourable environments driven by higher variability and lower temporal autocorrelation can also lead to increased additive genetic variance, thereby increasing the evolutionary potential of a trait[26,61,61,62,62–67]. The hypotheses for why such an increase in genetic variance could occur are reviewed in [60]. One is that selection is ineffective in removing mutations that are maladaptive only in rare environments[68]. Thus, exposure to novel environments will increase genetic variation and therefore heritability[26,69]. Determining the magnitude and frequency of this phenomenon in natural populations is an important focus for research, as the opposite effect is also known to occur[65,66,70–75].

The effect of environmental novelty on heritability, selection, and genetic variance depends also on the system-specific evolutionary history and relationship between environmental and genetic effects in producing phenotypes[60]. Contrary to above for example, some studies show that both environmental novelty and harshness can decrease additive genetic variance[65,66,70–75]. This decrease may occur if an unfavourable condition prevents individuals from expressing the underlying genetically determined benefits from a trait, for example due to lack of nutrition[71]. In such cases, selection could favour the regulation of gene expression such that alleles are not expressed in an unfavourable environment, for example by decreasing the heritability of traits underpinned by associated alleles[60]. In turn, depending on the mechanisms at play, evolutionary tracking may be either facilitated or hindered in environments with an increasing rate of change, variation, and/or autocorrelation. Whether or not a population is likely to successfully track a moving environmental optimum will in part determine the ability of plasticity to help bridge this gap.

3 Mechanisms of ecological response to changing environments: life history, plasticity and population dynamics

Environmental change impacts on population size and life history

Life history and population size impact both ecological dynamics and evolutionary trajectories [76,77], In turn, population size is inherently linked to adaptive potential, as larger populations have more standing genetic variation available for natural selection, [38,78] (see section 2). Thus, the importance of phenotypic plasticity in adaptive evolution depends on changes in population size, which also influences the likelihood of local extinctions [79–82]. Such impacts of population size depend on life history; long-lived species can persist longer at small population sizes than short-lived species, which can collapse quickly [83,84].

Much evidence shows that higher rates of environmental change lead to decreases in population size[85], suggesting that rates of local extinction rates of many bird and mammal species will increase as the rate of climate warming exceeds the rate of adaptive responses[86]. However, population size can increase in some species under higher rates of environmental change. For instance, bird species adapted to drier climates can utilize agricultural land and are predicted to persist in and colonize into drier habitats under climate change[87]. Mechanistically, however, the explicit links between increasing rate of environmental change and population dynamics remains largely unresolved.

The interplay between increasing environmental variability and population size has now been intensively studied both theoretically and empirically[88]. Despite the usual assumption that a more variable environment is detrimental for populations, recent syntheses across systems show that the effect of environmental variability is highly context-dependent and can have positive as well as negative effects on population growth rates [24,89]. Demographically-explicit theories have made important progress in elucidating the mechanisms for why increased environmental variability can have different influences on population size [90]. The mechanisms that produce the disparities in demographic responses to variable environments usually depend on system-specific density-dependent effects, which influence **transient dynamics** of population trends [91].

Temporal autocorrelation in the environment has gained much attention in population biology and climate change research[31,34]. Here too, the emerging message is that autocorrelated environments can have positive[92,93] or negative[93] impacts on population size and extinction risk, depending on life history strategies[94], and phylogenetic history[95]. For example, annual plants have lower extinction risks when the environment is more positively temporally autocorrelated compared to perennial plants[93]. Moreover, in some cases, population size itself can become more variable through time under positive environmental autocorrelations, thereby increasing extinction risk[34].

Environmental change impact role of within-generational plasticity

Plasticity and population dynamics are known to impact the ability of populations to evolutionarily track a moving optimum[39,96]. While selection works to decrease the phenotypic lag, plasticity can also reduce the size of this lag[40] (but see [10]). However, this impact of plasticity on lag size is complex, for plasticity itself can evolve, has different forms depending on the **life history strategies** of the population[97,98], and can be considered at the level of genes, individuals, populations, or species[99,100]. Even within these levels, there is disagreement about how different environments alter the ability of plasticity to affect lag in populations of different size[100]. How we judge the efficacy of plasticity to affect population dynamics depends on assumptions about its inherent costs and limitations[101] and how they interact with the three environmental parameters.

Often plasticity is assumed to buffer decreases in population size due to increasing rates of environmental change, although it is increasingly clear that this relationship is context dependent[100]. A key implicit assumption in moving optimum theory is that plasticity incurs some energetic cost[48,102] which depends on the type of trait (*e.g.*, morphology, phenology, physiology, behaviour) and the rate of environmental change. The cost of plasticity thus adjusts the critical limit of environmental change, producing a complex interaction between rate of environmental change and net benefit of plasticity[103,104].

Environmental variability also impacts the ability of plasticity to benefit population size and persistence. Although plasticity can mitigate the detrimental effects of environmental variability in some cases[105,106], individual-based simulations have shown that the magnitude of environmental fluctuations has surprisingly limited effects on population persistence[107]. The limitation of their results is in part because increased variation can decrease survival[108] without much effect on the amount of plasticity or amount of phenotypic lag.

Environmental temporal autocorrelation seems to have a clearer effect on the benefit of plasticity to population persistence than environmental variability. Both the theoretical and empirical literatures suggest that unreliable environmental cues, or low temporal autocorrelation, decrease the ability of plasticity to reduce extinction risk[101,109]. Here, we consider within-generational plasticity, but note that there is increasing interest in the evolution of plasticity over multiple generations[9]. More predictable fluctuations select for increased plasticity, suggesting that plasticity has a beneficial role for tracking moving optima[110].

4 Synthesis: when does plasticity help or hinder adaptive evolution?

Climate change will lead to changes in the rate, variation, and autocorrelation of environmental variables. Moving optimum theory provides a mechanistic approach to develop hypotheses about the impact of plasticity on adaptive evolution in different environments. It is clear that hypotheses such as the Bogert effect, Plasticity-First, and Baldwin hypothesis cannot be tested without controlling for the types of environmental change. This is because the facilitative role that plasticity might play for adaptive evolution in the face of environmental change depends on *how* the environment is changing. Each of the three environmental components (Fig. 1) influences the two broad categories of eco-evolutionary response mechanisms: 1) heritability, genetic variation, and selection, and 2) within-generation plasticity and population dynamics. The interaction between environmental change components and response mechanisms produces a rich breadth of hypotheses (Box 1); empirical and theoretical tests of these hypotheses will form a more integrative understanding of adaptive responses to a changing world.

Here, we leverage the mechanisms of evolutionary response that we have discussed to suggest a baseline of testable hypotheses for how the facilitative role of plasticity may change as environmental parameters change (Box 1; Figure 2). Our primary goal is to call attention to how plasticity's contribution to adaptive evolution depends on environmental context. Contradictory hypotheses abound; we contend that these in fact present focal targets for future empirical validation.

Box 1: Hypotheses for the Benefit of Plasticity on Adaptive Evolution in Response to Environmental Change

Current empirical and theoretical work allows us to define null hypotheses of how plasticity can impact adaptive evolution in response to changes in environmental mean rate of change, variation and autocorrelation. Each of these hypotheses utilizes moving optimum theory to infer how the relationship between phenotypic lag and adaptive tracking can be moderated by phenotypic plasticity. This interaction can result in a positive, negative or unimodal relationship between the environmental property and the benefit posed by plasticity for adaptive evolution.



Figure 2. Graphical hypotheses for the relationship between environmental properties and benefits of plasticity for adaptive evolution. Panel A [i-iii] describes the benefit of plasticity for adaptive evolution across an increasing rate of environmental change, Panel B [i-iii] describes this dynamic across increasing environmental variance, and Panel C [i-ii] across increasing temporal autocorrelation.

Hypothesis A[i]: The benefit of plasticity increases with increase in the rate of environmental change, eventually plateauing. Selection is weak when the mean environmental change is slow, and phenotypic lag is small. Population growth is consequently high, and heritability of fitness-related traits is high. In this scenario, plasticity adds little to adaptive tracking, and thus the costs of plasticity outweigh the benefits in decreasing the phenotypic lag. Conversely, when the mean environment changes too fast for adaptive evolution to track, and phenotypic lag is high, plasticity helps to 'catch up' with the moving optimum by allowing for the population to increase in size, and thus maintain the genetic diversity.

Hypothesis A[ii]: The benefit of plasticity decreases with increases in the rate of environmental change. Contrary to Hypothesis A[i], when selection is weak, lag load can increase because the population evolves more slowly. In this scenario, plasticity can bring the population phenotypic mean close to the selection peak at a low rate of environmental change. Conversely, as rate of mean environmental change increases, the limits of plasticity set by its costs (physiological toll and erosion of genetic diversity) may result in a limited role of plasticity for adaptive tracking. The population size may be small at high rates of environmental change, and plasticity may increase the chance of extinction due to drift by shifting the phenotypic average and thus shading the genetic variation from selection. Moreover, a high rate of environmental change can limit the efficacy of plasticity given the low predictability of the future environment.

Hypothesis A[iii]: The benefit of plasticity is maximised at an intermediate rate of environmental change, above (following A[i]) and below (following A[ii]) which its benefit decreases. Following moving optimum theory, there is an intermediate rate of environmental change at which the balance between selection strength and population persistence is optimal.

Hypothesis B[i]: The benefit of plasticity to adaptive evolution increases with increasing environmental variation. As the environment becomes more variable, plastic responses in physiology, life history, phenology, and/or behaviour can dampen the detrimental effects of unpredictable fluctuations, thereby preventing extinction. This buffering would afford the population more time to reach its adaptive peak via adaptive evolution. This benefit would eventually cross a point of diminishing returns, as when the environment becomes too variable, the costs involved in plastic responses may outweigh their benefits in part due to the lack of predictability in the temporal environment. Moreover, at a highly variable environment with a stationary mean, evolution may serve to be nonadaptive, and plasticity can allow the genotypic mean to remain near the environmental mean amidst the environmental variability.

Hypothesis B[ii]: The benefit of plasticity to adaptive evolution decreases with increasing environmental variation. In an environment with a small amount of variation, plasticity works together with evolution to fix traits helpful in the new environment. As the environment becomes more variable, phenotypic plastic responses may drive a disconnect between phenotypic selection and genotypic selection, ultimately making the genetic variation in the population maladapted to future environmental conditions. In other words, plasticity might help a population that is stuck in a valley or a local peak to find a global peak on a fitness landscape when the environment is moderately variable; if the environment is too variable, peak searching might be disrupted too much—and peaks themselves would be shifting on the landscape.

Hypothesis B[iii]: The benefit of plasticity to evolution is highest at low and high amounts of environmental variability. The ability of the trait mean in the population to reach the peak of fitness landscapes via adaptive evolution may be optimal at an intermediate level of environmental variance. In this case, the facilitative role of plasticity would be low at an intermediate level of environmental variance if it masks genetic variance of the population from selection, or shifts the phenotypic average.

Hypothesis C[i]: The benefit of plasticity to adaptive evolution increases with increasing temporal autocorrelation. Higher autocorrelation in the environment corresponds to higher reliability of temporal cues and thus higher predictability of future environmental states. Therefore, plastic responses can more accurately track moving selection targets, and aid adaptive tracking. In addition, adaptive evolution may be less likely to occur in isolation in highly autocorrelated environments.

Hypothesis C[ii]: The benefit of plasticity to adaptive evolution decreases with increasing temporal autocorrelation. Autocorrelation at temporal lags that are not in resonance (similar lengths of time) with paces of life history can increase extinction risk. This could lead to a population existing in an unfavourable environment for long periods (reducing temporal refugia), and plasticity could decrease the genetic variation upon which selection can act. Thus, the ability for plasticity to help adaptively track moving optima decreases.

5 Concluding remarks

Although there is a growing literature assessing hypotheses related to the Baldwin effect, Plasticity-First hypothesis, and the Bogert effect[5,10,21,111], no papers have systematically compared and contrasted, theoretically or experimentally, how these expectations differ across the three parameters of environmental change (rate of change, variation, autocorrelation). Here we pose a framework yielding testable hypotheses to encourage both experimental and theoretical research that takes into account simultaneous variation in plasticity and genetics in response to changing environments.

There are increasing reports of phenotypic and genotypic data from natural populations exposed to changing environmental regimes [41,112,113]. They allow direct assessment of genetic and plastic adaptive processes over time and under different environmental scenarios. Therefore, the time is ripe to reassess our understanding of the relative roles of phenotypic evolution by selection and plasticity. Here, we have introduced an integrative framework that delineates null hypotheses for when and how much plasticity might be employed for adaptive evolution and persistence under realistic types of environmental change. With more explicit theories and field measurements of how the rate of change, variability, and temporal autocorrelation of the environment impact the mechanisms of evolutionary responses, we may reach a deeper understanding of species responses in the Anthropocene.

Outstanding Questions

How can the effect of plasticity on evolution be quantified? We suggest that manipulating the rate of mean change, variability, or autocorrelation with appropriate controls could elucidate the interplay between plasticity and selection. Importantly, focusing on how the chosen environmental parameter influences heritability, selection, life history, or population size can clarify the mechanism of influence. In order to test these hypotheses, one must first define the types of environmental change that may be experimentally manipulated, the genetic mechanisms that affect the trait(s) of interest (section 2), and type of plasticity in the population (section 3).

Can knowledge about the context-dependent role of plasticity in adaptive evolution aid in land management and determine conservation priorities? We suggest that simultaneously estimating the environmental change components reviewed in this article and measuring both the evolutionary and phenotypic plastic responses in the relevant system will unlock new insights into the ability of populations to persist under climate change.

Which hypotheses of the potential role of plasticity are most robust and accurate? This question cannot yet be answered, for the hypotheses we have put forth, which are stimulated by both eco-evolutionary theory and evidence, are thus far untested with respect to relative prevalence or accuracy. New information about the mechanisms underlying ecological and evolutionary response to different types of environmental change will raise new questions regarding when plasticity's potential role in adaptive responses might be greatest.

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Glossary

Adaptive evolution : genetic changes in a population that confer directional changes in a fitness-related trait. The direction of trait evolution is determined by the new phenotypic optimum, whilst the magnitude

of change results from the strength of selection (genetic variation and heritability).

Baldwin effect : a novel state of a trait that emerges/changes via plastic mechanisms that is subsequently reinforced by genetic mechanisms that stabilize the trait across generations.

Bogert effect : the effect of plasticity in masking genetic variation from selection. Common examples include thermoregulatory behaviours in ectotherms.

Breeder's equation : can be used to quantify the expected difference in mean trait value as the product of the heritability of the trait (h^2) and the selection differential the trait is exposed to (S): $Z = h^2 S$.

Critical rate of change : The maximum rate of environmental change the population can handle. Exceeding this limit inevitably results in a population decline towards extinction.

Environmental changes : a shift in abiotic (e.g., temperature and precipitation) and/or biotic factors (e.g., predation risk and community structure) that shifts the phenotypic optimum of a trait.

Environmental novelty : the degree to which biotic and abiotic factors differ between present and past. This can be quantified by the distance the phenotypic optimum has moved relative to the optimum in a normal environment.

Lag load : the gap between the moving phenotypic optimum and the mean trait value in the population.

Life history strategies : the suite of vital rate functions (e.g., survival, growth, reproduction) and associated phenotypes (e.g., morphology, behaviour, offspring investment) that work together to optimize the fitness of individuals and viability of populations over time.

Moving optimum theory : a body of work showing that, at any point in time, there is a phenotypic optimum that maximizes the fitness of individuals. This optimum can change over time due to biotic and abiotic factors. In turn, populations track the moving optimum, at a certain lag, via plasticity and/or adaptive evolution.

Phenotypic lag : a gap between the moving phenotypic optimum and the population mean trait.

Phenotypic optimum : the phenotype that maximizes fitness at a point in time.

Phenotypic plasticity : environmentally induced changes in an individual's phenotype without changes in its genetic makeup.

Plasticity-first hypothesis : genetically based variation in plasticity among individuals in a population responds to selection in a novel environment. This initial variation in plasticity allows for the population to persist when it would not have been able to do so if it were plastic and then to respond to selection.

Rate of mean change : the direction and magnitude of differences in average environmental values (e.g., temperature and precipitation) over time.

Temporal autocorrelation : the correlation of terms in series separated by a time interval. Degree of autocorrelation is often described by the "colour of noise" where negative autocorrelation yields blue noise, zero autocorrelation yields white noise and positive autocorrelation yiels red noise.

Temporal refugia : a period of time where the degree/number/duration of perturbations in the environment that negatively affect fitness are reduced, allowing for intermittent rescues in population size and structure.

Trait heritability : the proportion of trait variance that is a consequence of additive genetic variance.

Transient dynamics : short-term fluctuations in population size/structure that arise due to both (1) perturbations in the structure and/or size of the population and (2) probabilistic events (e.g., survival and reproduction) as the population approaches an equilibrium.

Variability : the variance of an environmental variable (e.g., temperature and precipitation) value over time.

Vital rates : a component of fitness (e.g., survival, growth, reproduction, stasis) that varies across the structured life-cycle of an organism (i.e., age, stage, size).

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