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Opinion

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

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To forecast extinction risks of natural populations under climate change and direct human impacts, an integrative understanding of both phenotypic plasticity and adaptive evolution is essential. To date, the evidence for whether, when, and how much plasticity facilitates adaptive responses in changing environments is contradictory. We argue that explicitly considering three key environmental change components – rate of change, variance, and temporal autocorrelation – affords a unifying framework of the impact of plasticity on adaptive evolution. These environmental components each distinctively effect evolutionary and ecological processes underpinning population viability. Using this framework, we develop expectations regarding the interplay between plasticity and adaptive evolution in natural populations. This framework has the potential to improve predictions of population viability in a changing world.

Highlights

Global biodiversity is jeopardised by unprecedented environmental change, the hallmark of the Anthropocene. To estimate the extinction risks of species, understanding how individuals and populations respond to changing environments is crucial.

Adaptive evolution and phenotypic plasticity are two key mechanisms by which natural populations avoid extinction in the face of environmental change. However, the relative roles and interplay between the two are still unresolved.

Whether plasticity hinders (H1) or facilitates (H2) adaptive evolution has been ardently researched, but without cross-study standardization of how changing environments impact whether (H1) or (H2) is more likely over time.

We propose an integrative framework based on how key environmental components influence the 'building blocks' of ecoevolutionary responses to examine when plasticity aids or hinders adaptive evolution. We synthesise key microevolutionary and ecological processes regarding how natural populations respond to environmental change.

Studies may benefit from this framework to deepen our understanding of how plasticity influences adaptive evolution by reframing H1 and H2 in the context of environmental change, and will thus increase our ability to forecast extinction risks in the Anthropocene.

Plasticity and adaptation in a changing world

Understanding, quantifying, and predicting the ability of organisms to adapt to changing environments is at the core of ecoevolutionary research [1–4]. In the face of unprecedented **environmental change** (see Glossary), natural populations, especially those with limited mobility/dispersal, can avoid extinction via **phenotypic plasticity** and/or **adaptive evolution** [4]. However, our understanding of the interplay between adaptive evolution and plasticity in changing environments remains limited [1,5–8]. This limitation is not trivial, for plasticity can itself evolve [9], be adaptive, or nonadaptive [10], and have differing effects on adaptive evolution [11,12].

For decades, researchers have theorised whether plasticity facilitates or hinders adaptive evolution [9,13]; the evidence is contradictory, and general patterns have yet to emerge [5,10,11,14,15]. The primary conflicting hypotheses for whether plasticity facilitates or hinders adaptive evolution are:

- (H1) Plasticity weakens directional selection by masking genotypic variation (e.g., **Bogert effect** [16]), thus slowing the rate of genetic change [5,17–19].
- (H2) Plasticity facilitates evolution by allowing the population to persist under environmental change long enough for genetic change to occur [20–22] (e.g., **plasticity-first hypothesis** [22] or **Baldwin effect** [20]).

This debate remains unresolved. Despite cases where theoretical predictions agree with empirical findings [5,10,11,14,15,23], we lack a general framework to establish the context-dependence of plasticity's impact alongside climate change. Here, we introduce an environmentally explicit framework that allows for the development and testing of hypotheses regarding when and how plasticity interacts with evolution. We highlight three environmental change components: **rate of mean change**, **environmental variability**, and **temporal autocorrelation**. These environmental

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components distinctly impact evolutionary and ecological processes as mechanisms of population response [24–26] and are widely documented consequences of climate change [27–29]. Consequently, there is an urgent need to integrate the effects of environmental change in a generalizable way. This will allow ecologists and evolutionary biologists to better contextualise, mechanistically understand, predict, and compare their findings.

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Moving optimum theory links environmental change to the resulting evolutionary responses according to changes in phenotypic traits. 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. That is, the mean phenotype must remain close to the theoretical **phenotypic optimum**. In this context, a **phenotypic lag** between the mean phenotype and the optimum phenotype may emerge which, if too large, increases extinction risk [30,31]. Evolutionary processes (e.g., selection, genetic variation) and ecological processes (e.g., life history, within-generation plasticity, and population dynamics) together influence how far a population can lag and persist. Thus, the contribution of plasticity to population persistence and adaptation is largely determined by this phenotypic lag.

We argue that H1 and H2 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 adaptive evolution, we specify the links among the type of environmental change, plasticity, and adaptive evolution. Thus, we utilise theoretical and experimental work to:

(i) Assess how three key components of environmental change (rate of mean change, variability, and temporal autocorrelation) each alter the evolutionary and ecological mechanisms behind phenotypic tracking of a moving optimum.
(ii) 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.

Mechanisms of evolutionary response to changing environments: interactions between environmental change and genetic variation, heritability, and selection

To understand the role of plasticity in adaptive evolution, one needs to consider how different environmental components 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. The genetic architecture of a trait under selection will, in part, determine the potential for adaptive evolution and ecoevolutionary dynamics [32]. Most traits that mediate population dynamics are determined by multiple genes, each of which typically has a small effect (quantitative traits) [32,33]. One way to assess whether or not a quantitative trait may evolve is via the **breeder's equation**, which equates the change in a trait to the selection differential times its narrow-sense heritability. Heritability is a function of both genetic variation [34,35] and the environment in which that variation is expressed [36]. 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 ([37], but see [38]). In the following sections, we discuss literature that addresses how rate of mean change, variability, and temporal autocorrelation in the environment each influence heritability, genetic variation, and selection. By considering the environmental impacts on these evolutionary mechanisms, we aim to understand the ability of genetic change to track a fitness optimum in changing environments. This understanding informs the importance 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 a small **lag load** [39,40]. As the rate of environmental change increases, selection strengthens, and the population can track the moving optimum with a consistent phenotypic lag [41]. In this range of environmental change, additive genetic variance and heritability can also increase [39,42]. In this case, up to a certain intermediate rate of environmental change, genetic variation and evolutionary potential may be expected to increase. This can occur simply due to higher additive genetic variance and thus 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 trait optimum, changes too quickly [39,41,43]. Here, the phenotypic lag increases, which can lead to decreased fitness and eventually local extinction [44]. As such, the mean time to extinction in a natural population decreases as the rate of environmental change increases beyond the optimal rate [39]. Thus, the rate of environmental change in evolutionary experiments and theory is key to assess the potential benefit of plasticity on adaptive evolution.

Impact of environmental variation and temporal autocorrelation on underlying genetics

Moderate environmental variation can optimise selection, and ultimately evolutionary tracking [45,46] (but see [2]). In contrast, the ability of populations to evolutionarily track a shifting adaptive peak can increase with greater temporal autocorrelation [25]. Moreover, theoretical work predicts that positively autocorrelated environmental fluctuations can increase additive genetic variance and its ability to reduce genetic load. This increase in genetic variance allows the mean phenotype to track a changing environment more closely [25]. Thus, evolutionary potential may be higher in temporally autocorrelated environments than in uncorrelated environments.

The evolutionary effects of environmental variability and autocorrelation are often framed in terms of increasing frequencies of novel and unfavourable environments [47]. Greater environmental variability and lower temporal autocorrelation expose individuals to environments that are novel and often unfavourable, and their impact on evolutionary response is mixed depending on other factors at play [47]. In addition, a direct consequence of higher variability and higher autocorrelation is that populations spend less time in **temporal refugia** [29], which reduces fitness.

Conversely, theoretical and empirical research have shown that exposure to unfavourable environments can also lead to increased additive genetic variance, thereby increasing the evolutionary potential of a trait [47]. This increase in additive genetic variance can occur when selection is ineffective at removing mutations that are maladaptive only in rare environments [47,48]. Moreover, novel environments can reveal cryptic, or previously unexpressed genetic variation [12]. Thus, exposure to novel, and unfavourable environments could increase genetic variation and therefore heritability.

Determining the magnitude and frequency that genetic variance increases in response to **environmental novelty** and harshness is non-trivial, as the opposite effect can also occur [47,49–51]. The effect of environmental novelty and harshness depends on the system-specific evolutionary history, and interaction between environmental and genetic effect [47]. For example, both environmental novelty and harshness can decrease additive genetic variance if an unfavourable condition prevents individuals from expressing the underlying genetically determined benefits from a trait [51]. In such cases, selection could favour the regulation of gene expression such that alleles are not expressed in an unfavourable environment. This lack of expression in

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 stabilise the trait across generations. This line of thinking has been used to describe a range of traits, from developmental variation in house finches to multicellularity [81].

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

Breeder's equation: an equation that quantifies the expected difference in mean trait value as the product of the narrow sense heritability, or the proportion of trait variation attributed to additive genetic effects (h^2) and the selection differential the trait is exposed to (S) : $\Delta Z = h^2 S$.

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.

Demographic buffering: a strategy where populations have negative covariance of a vital rate's impact on population growth rate and its variance over time.

Environmental change: a shift in abiotic factors (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 novelty can be quantified by the distance the phenotypic optimum has moved relative to the optimum in the previous environmental state.

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

Lag load: the distance between the average fitness of a population and its local adaptive peak. The greater the lag load, the higher the selective pressure.

unfavourable environments may occur through decreasing the heritability of traits underpinned by associated alleles [47]. Here, heritability could decrease when additive genetic effects determine a trait such as body size. If unfavourable conditions decrease growth rate, this decrease can lead to a reduction in the additive genetic variance.

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 necessity of plasticity to help bridge this gap. Thus, the impact of the environmental change variables on evolutionary tracking should be considered when addressing H1-2.

Mechanisms of ecological response to changing environments: interactions between environmental change and life history, plasticity, and population dynamics

Environmental change impacts on population size and life history

The importance of phenotypic plasticity in adaptive evolution depends on changes in population size, which influences the likelihood of local extinctions [52,53]. Such impacts of population size depend on **life history strategies**; for example, long-lived species can persist longer at small population sizes than short-lived species, whose populations can collapse quickly [54,55]. Furthermore, these strategies can determine the rate of trait evolution [8]. It is therefore vital to consider the impact of different environmental components on population dynamics and life history to understand the impact of the type of environmental change on the interplay between plasticity and adaptive evolution.

Higher rates of mean environmental change typically lead to decreases in population size [56]. This finding suggests that local extinction will increase as the rate of climate warming exceeds the rate of adaptive responses. However, population size can increase in some species under higher rates of environmental change. For instance, bird species adapted to drier climates can utilise agricultural land and colonise drier habitats under climate change [57]. Demographic theories can help to explain such contradictory empirical cases: for instance, differences in life history and population structure (e.g., size, age) can translate a rate of change in a trait (e.g., reproduction) into different outcomes of population growth rate.

The interplay between increasing environmental variability and population size has now been intensively studied both theoretically and empirically [58]. It is usually assumed that a more variable environment is detrimental for populations. However, recent syntheses show that the effect of environmental variability can have both positive and negative effects on population growth rates [2,59]. For example, disparities in population size responses to environmental variability are influenced by differences in the magnitude of density dependence [60]. Density dependence varies between systems due to species-specific physiology or life history [60,61]. Such differences cause further disparities in **transient dynamics** of population trends [62]. Further, nonlinear relationships between environmental states and **vital rates** across st/age classes within populations ('**reaction norms**') can induce varying **demographic buffering** capabilities across populations and species [63,64]. Variation in degrees of demographic buffering via plasticity of vital rates, can contribute to the observed inconsistencies in comparative analyses of population dynamics in variable environments [65].

Temporal autocorrelation in the environment has gained much attention in population biology and climate change research [29,66]. Here too, the emerging message is that autocorrelated

Life history strategies: the age-specific schedules of vital rates (see below) and associated phenotypes (e.g., morphology, behaviour, offspring investment) that determine the fitness of individuals and viability of populations.
Moving optimum theory: a body of work showing that, at any point in time, there is a phenotypic optimum that maximises 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 maximises fitness at a point in time.
Phenotypic plasticity: environmentally induced changes in an individual's phenotype without changes in its genetic makeup. These changes can be adaptive, or nonadaptive (have a neutral or negative impact).
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.
Reaction norms: the effect of an environmental factor on the value of a trait.
Temporal autocorrelation: the correlation of terms in series separated by a time interval. High autocorrelation refers to a case where successive values are highly correlated, a negative autocorrelation indicates an inverse relationship between two variables, and no autocorrelation refers to a case where successive values are uncorrelated.
Temporal refugia: a period in which the degree/number/duration of perturbations in the environment that negatively affect fitness is reduced, allowing for intermittent rescues in population size and structure.
Transient dynamics: short-term fluctuations in population size/structure that arise due to both (i) perturbations in the structure and/or size of the population and (ii) probabilistic events (e.g., survival and reproduction) as the

environments can have positive [67,68] or negative [68] impacts on population size and extinction risk, depending on life history strategies [69] and phylogenetic history [70]. For example, annual plant populations have lower extinction risks than perennial populations when the environment is positively temporally autocorrelated [68]. In some cases, long stretches of adverse conditions caused by positive environmental autocorrelation can exacerbate extinction risk [66]. One example is when highly positively autocorrelated fluctuations cause multiple generations to experience negative growth [12]. Conversely, highly autocorrelated environments could allow for an increasing population size, as populations may be better able to track the optimum trait value [44]. And lastly, simulations of density-independent stage-structured populations suggest that pace-of-life and degree of iteroparity positively correlate with a population's sensitivity to environmental autocorrelation [70].

population approaches a stationary equilibrium.
Vital rate: a demographic process (e.g., survival, growth, reproduction). Vital rate values typically vary across the structured life cycle of an organism (e.g., age, stage, size).

Environmental change impacts on role of within-generational plasticity

While selective pressures tend to decrease phenotypic lag, so can plasticity [30,71] (but see [10]). However, the impact of plasticity on lag size is complex, for plasticity itself can evolve [72], has different forms depending on the life history strategies [72,73], and level of biological organisation [74,75]. Even within these levels, there is disagreement about how different environments alter the ability of plasticity to affect lag in populations of different sizes [75]. How we judge the efficacy of plasticity to affect population dynamics depends on assumptions about plasticity's inherent costs and limitations [76] and how they interact with the three environmental parameters (Figure 1).

Increasing rates of environmental change have been theorised to decrease the benefit of plasticity when the environment becomes extreme. However, much of this work utilised a categorical framework such as 'abrupt' and 'gradual', as opposed to a continuous measure [26]. A key implicit assumption in moving optimum theory is that plasticity can buffer decreases in population size, but incurs some energetic cost [37,77]. This cost depends on the type of trait (e.g., morphology, phenology, physiology, behaviour) and the rate of environmental change [75]. Moreover, the trade-off between the ability of plasticity to buffer environmental changes and its costs can be impacted by correlations between trait values as well as the slopes of their respective reaction norms. In turn, these trait covariances and reaction norms can influence the interplay between selection on mean trait values, and changes in plasticity [78]. 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 [30].

Environmental variability also impacts the ability of plasticity to benefit population size. Although plasticity can mitigate the detrimental effects of environmental variability in some cases, individual-based simulations have shown that the magnitude of environmental fluctuations has surprisingly limited effects on population persistence [79]. This has also been shown in herbivory defence traits of wild radish populations, cementing the idea that although plasticity often correlates with environmental variation, the interplay between environmental variation and plasticity is non-trivial [80,81].

Environmental temporal autocorrelation seems to have a more apparent effect on the benefit of plasticity to population persistence than environmental variability. The theoretical and empirical literature suggests that unreliable environmental cues decrease the ability of plasticity to reduce extinction risk [12,76,82]. In addition, we note that epigenetic modifications can relay a predictive adaptive response to the next generation(s), which is likely to be advantageous in highly predictable environments [83], warranting further study. More predictable fluctuations select for increased plasticity, suggesting that plasticity has a beneficial role for tracking moving optima [84]. Moreover, less predictable environments have been hypothesised to decrease – and even reverse – the potential beneficial role of plasticity on population growth rate [12].

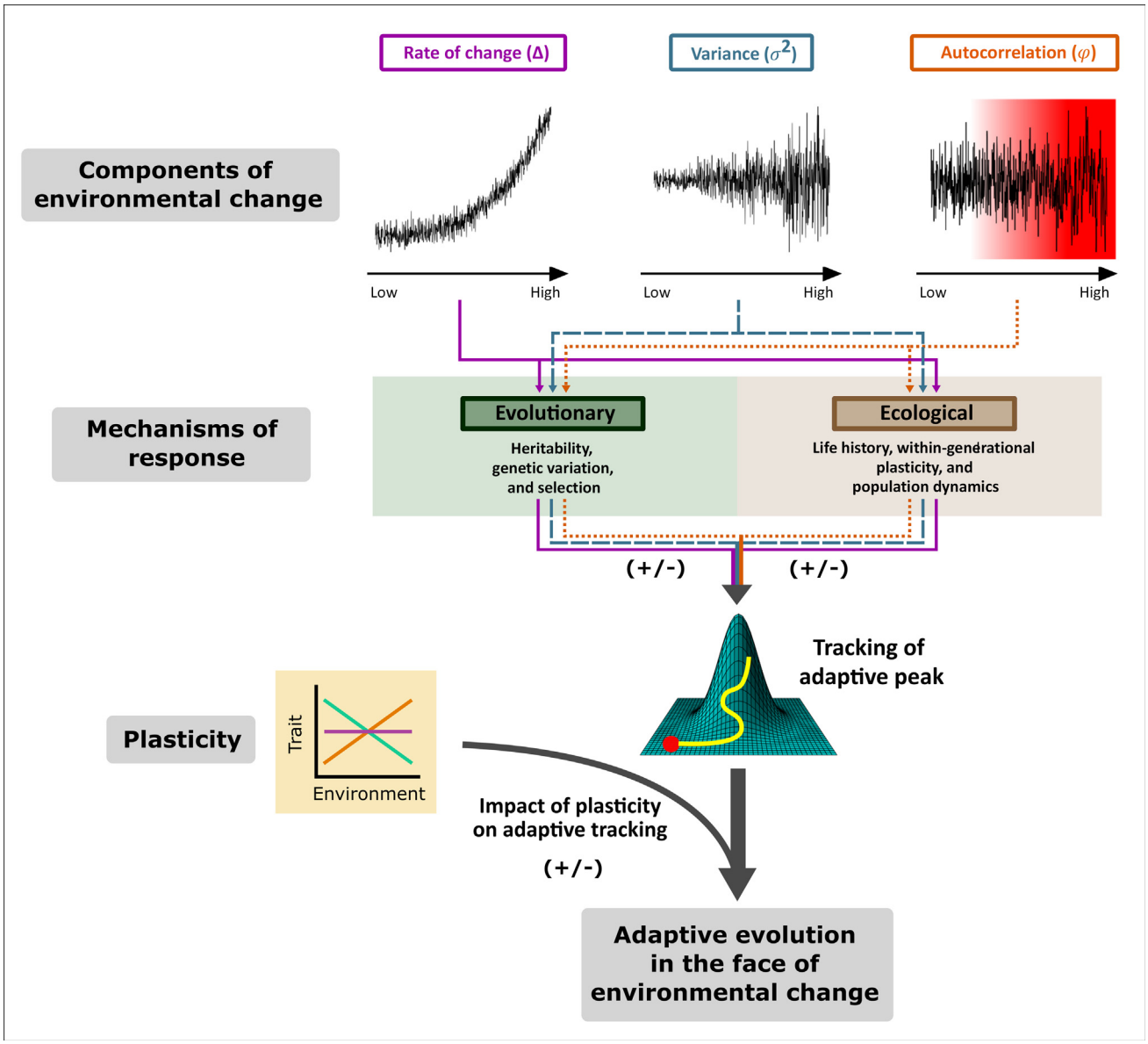

Figure 1. Framework to assess the environment-dependent impact of phenotypic plasticity on adaptive evolution. First, the three key environmental change components (rate of change, variance, and autocorrelation) each influence the two broad categories of mechanisms through which natural populations respond to changing environments: evolutionary and/or ecological processes. Evolutionary processes include heritability, genetic variation, and natural selection. Ecological processes encompass demographic dynamics driven by fluctuations in population size, within-generational plasticity, and life history. At the core of our conceptual framework, all of these mechanisms influence whether and how well a population can track the fitness peak, which moves through trait space 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 contextualise the magnitude and direction of plasticity's impact on population persistence and adaptive evolution via mechanistic links.

Synthesis: when does plasticity help or hinder adaptive evolution?

Climate change is predicted to 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 changing

environments. In this context, H1 and H2 cannot be tested without controlling for the types of environmental change. 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 (Figure 1) influences the two broad categories of ecoevolutionary response mechanisms, as discussed in earlier sections. 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.

Box 1. Hypotheses regarding the benefit of plasticity on adaptive evolution in response to increasing mean rate of environmental change

Each of these hypotheses utilises moving optimum theory to infer how the relationship between phenotypic lag and adaptive tracking can be moderated by phenotypic plasticity alongside an increasing rate of mean environmental change (Figure I).

Hypothesis A[i]

The benefit of plasticity increases with rising rates of environmental change, eventually plateauing. Selection is weak when environmental change is slow, and phenotypic lag is small. Population growth is consequently high, and heritability of fitness-related traits is also high. In this scenario, plasticity adds little to adaptive tracking, 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 the population 'catch up' with the moving optimum by allowing the population to increase in size, and thus maintain the genetic diversity.

Hypothesis A[ii]

The benefit of plasticity decreases with increasing rates of environmental change. Contrary to Hypothesis A[i], when selection is weak, lag load can increase. In this scenario, plasticity can bring the 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 (i.e., physiological toll and masking of genetic diversity [76,81]) may result in a limited role of plasticity for adaptive tracking. If population size is small at high rates of environmental change, plasticity can increase the chance of extinction due to drift by shifting the phenotypic average and thus shading the genetic variation from selection. This results in the maintenance of maladapted individuals and further decreases the population size. 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.

To test these hypotheses, we must first shift our thinking regarding the rate of environmental change from a categorical to a continuous framework. For example, increases in temperature and salinity can be simulated experimentally and considered using multiple rates of change [26]. Ideally, the trait or vital rate of interest should be assessed at the individual level within and across generations to estimate plasticity and evolution. The amount of plasticity and genetic change can then be compared across the different environmental levels. Ectotherms such as fruit flies (e.g., *Drosophila melanogaster*), phytoplankton (e.g., *Microcystis aeruginosa*), or nematodes (e.g., *Caenorhabditis elegans*) pose ideal systems to study these effects, given their short generation time and the ease in modifying their environment in a laboratory setting [85–87]. Moreover, given their small size, organism such as these allow for research into less studied levels of organization: populations and communities [26,81].

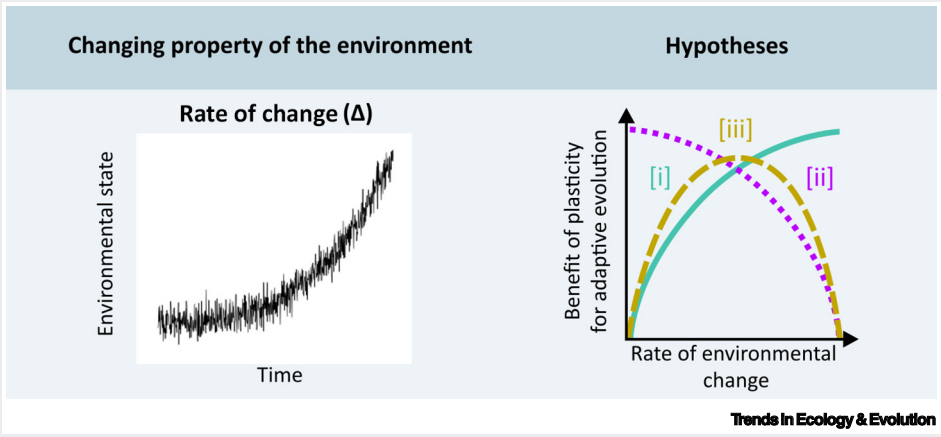

Figure I. Hypotheses for the relationship between the mean rate of environmental change and benefit of plasticity for adaptive evolution. The left side of the panel depicts an increasing rate of environmental change over time. The right side shows the graphical Hypotheses [i–iii], which describe [i] increase, [ii] decrease, and [iii] intermediate suboptimal benefit of plasticity for adaptive evolution across an increasing rate of environmental change.

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 (see Boxes 1–3 and the figures therein). 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 2. Hypotheses regarding the benefit of plasticity on adaptive evolution in response to increasing environmental variation

As in Box 1, each of these hypotheses utilises moving optimum theory, here determining the impact of increasing environmental variation on plasticity's role in adaptive evolution (Figure I).

Hypothesis B[i]

The benefit of plasticity to adaptive evolution increases with increasing environmental variation. As the environment becomes more variable, plastic responses can dampen detrimental effects of unpredictable fluctuations, thereby preventing extinction [71,72,75]. Buffering can 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 of plastic responses may outweigh their benefits. This decrease in the benefit of plasticity is in part due to the lack of predictability in the temporal environment. Moreover, in a highly variable environment with a stationary mean, evolution may be nonadaptive [2,88], and thus plasticity may 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 low variation, plasticity works together with evolution to fix advantageous traits for the new environment. As the environment becomes more variable, 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 more flexibly explore the fitness landscape, therefore avoiding being stuck in a valley or a local peak, and instead finding a global peak when the environment is moderately variable. If the environment is too variable, however, 'peak-searching' can be disrupted even with plasticity because the landscape itself shifts quickly.

Hypothesis B[iii]

The benefit of plasticity to evolution is highest in low and high 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.

As in Box 1, more experimental and theoretical work would help address the mechanisms underlying Hypothesis B[i]–[iii]. For instance, the impact of temperature variation on the grass *Brachypodium distachyon* is being studied using greenhouse experimental settings [89]. Systems like this, where researchers are already quantifying plastic traits and the impact of environmental variability, are ideal to test these hypotheses. Moreover, although controlled greenhouse and laboratory studies are necessary to improve understanding of plasticity's impact on adaptive evolution, they may obscure potential costs of plasticity [81]. Thus, studies that increase in realism from greenhouses to the field are necessary, and model grass species pose ideal candidates for work at both scales [90].

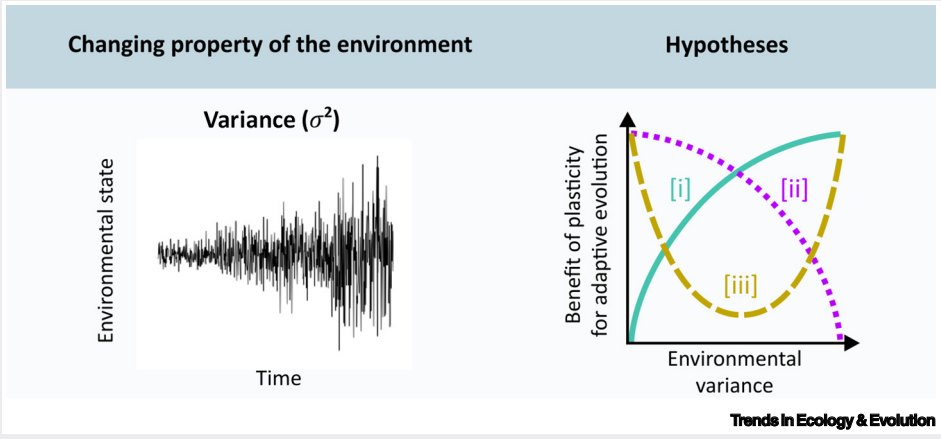

Figure I. Hypotheses for the relationship between the amount of environmental variation and benefit of plasticity for adaptive evolution. The left side of the panel depicts an increase in environmental variation over time. The right side of the panel shows Hypotheses [i–iii], which describe an [i] increasing, [ii] decrease, or [iii] intermediate optimal in benefit of plasticity for adaptive evolution with increasing environmental variance.

Box 3. Hypotheses regarding the benefit of plasticity on adaptive evolution in response to increasing environmental temporal autocorrelations

As in Boxes 1 and 2, we construct hypotheses regarding the impact of environmental autocorrelation on the potential benefit of plasticity for adaptive evolution, and adaptive tracking (Figure I).

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 [82]. Therefore, plastic responses may 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 can occur at various temporal lags [29] and the length of the lag can be out of sync with the pace of life history (e.g., generation time) of the focal species. In such case greater environmental autocorrelation might lead to the population existing in unfavourable conditions for long periods of time. If the populations stay in unfavourable conditions for extended periods, it can see a reduction in genetic variation and increase in extinction risk. Thus, the ability for plasticity to help adaptively track optima may decrease.

To test hypotheses C[i]–[ii], different levels of temporal autocorrelation must be generated. The impacts of temporal autocorrelation on life history, population dynamics, and plasticity have been studied [66,70,82]. However, to test hypotheses C[i]–[ii], controlled studies across generations need to be conducted to assess a variety of autocorrelation scenarios on intragenerational and intergenerational adaptation. In addition to systems recommended in Boxes 1 and 2, marine invertebrate systems such as *Bugula neritina,* which are likely to be impacted by varying temporal autocorrelation [91], would pose an ideal system to test these hypotheses. To test hypotheses C[i]–[ii], we also need theoretical models parameterised to estimate the changing impacts of temporal autocorrelation, in addition to experimental studies in controlled environments.

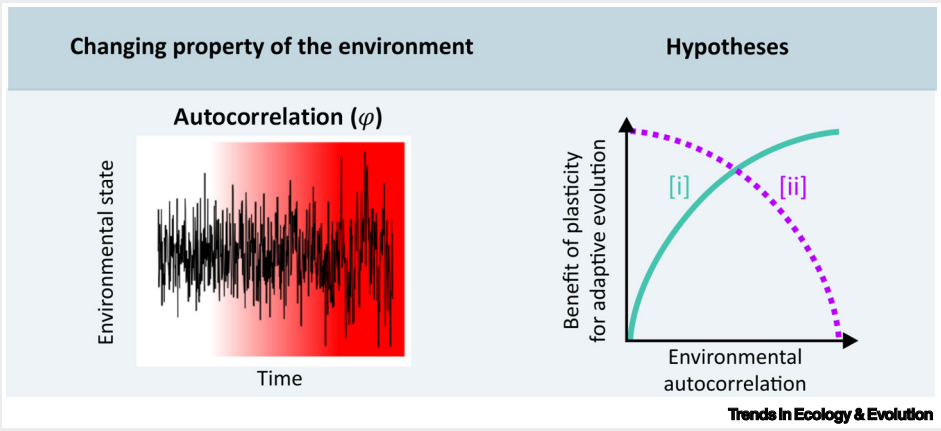

Figure I. Hypotheses for the relationship between temporal autocorrelation and benefit of plasticity for adaptive evolution. The left side of the panel depicts an increasing temporal autocorrelation in the environmental state over time. The right side of the panel shows Hypotheses [i–ii], which describe an [i] increase or [ii] decrease in the benefit of plasticity for adaptive evolution with increasing temporal autocorrelation.

Concluding remarks

A growing number of studies have tested the predictions generated from H1 and H2 (e.g., the Baldwin effect, plasticity-first hypothesis, and Bogert effect) [5,10,22,92]. Yet, as far as we know, no study to date has systematically compared and contrasted, theoretically or experimentally, how these predictions differ across the three parameters of environmental change (rate of change, variation, autocorrelation) (see Outstanding questions). 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

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 these environmental drivers impact heritability, selection, genetic variability, within-generational plasticity, life history, or population size can clarify the mechanism of influence on plasticity's impact on adaptive evolution. 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 (see section 'Mechanisms of evolutionary response to changing environments: interactions between environmental change and genetic variation, heritability, and selection'), and type of plasticity in the population (see section 'Mechanisms of ecological response to changing environments: interactions between environmental change and life history, plasticity, and population dynamics'). Specifically, progress must be made to further understanding of related mechanisms such as epigenetic changes, the role of cryptic genetic variation, as well as the prevalence of costs of plasticity.

Which hypotheses (Boxes 1–3) 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 ecoevolutionary theory and evidence, are thus far untested regarding their relative prevalence or accuracy. Thus, the need for experimental data, both in the laboratory and in natural settings, is vital to increase our understanding of the relative prevalence of each prediction. Moreover, new information about the mechanisms underlying ecological and evolutionary responses to different types of environmental change will raise new questions regarding when plasticity's potential role in adaptive responses might be greatest.

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

environments. We argue that autocorrelation, the least understood facet of environmental change in regard to the interplay between plasticity and evolution, deserves further exploration, in tandem with rate of change and variation. Specifically, the scientific community will gain key insights from scaling laboratory experiments with autocorrelation treatments to natural environments. Thus, we recommend a special focus be placed here, given expected increases in autocorrelation (with local variation) in both marine and terrestrial systems due to climate change.

the environmental change components reviewed in this article and measuring both the evolutionary and phenotypic plastic responses in the relevant system can unlock new insights into the ability of populations to persist under climate change.

Phenotypic and genotypic data from natural populations exposed to changing environmental regimes are becoming increasingly common. These data 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 hypotheses for when and how much plasticity might facilitate 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 (see Outstanding questions), we may reach a deeper understanding of species responses in the Anthropocene.

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Declaration of interests

No interests are declared.

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