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Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes

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Review



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Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes

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Theory suggests that evolutionary changes in phenotypic plasticity could either hinder or facilitate evolutionary rescue in a changing climate. Nevertheless, the actual role of evolving plasticity in the responses of natural populations to climate change remains unresolved. Direct observations of evolutionary change in nature are rare, making it difficult to assess the relative contributions of changes in trait means versus changes in plasticity to climate change responses. To address this gap, this review explores several proxies that can be used to understand evolving plasticity in the context of climate change, including space for time substitutions, experimental evolution and tests for genomic divergence at environmentally responsive loci. Comparisons among populations indicate a prominent role for divergence in environmentally responsive traits in local adaptation to climatic gradients. Moreover, genomic comparisons among such populations have identified pervasive divergence in the regulatory regions of environmentally responsive loci. Taken together, these lines of evidence suggest that divergence in plasticity plays a prominent role in adaptation to climatic gradients over space, indicating that evolving plasticity is also likely to play a key role in adaptive responses to climate change through time. This suggests that genetic variation in plastic responses to the environment ($G \times E$) might be an important predictor of species’ vulnerabilities to climate-driven decline or extinction.

This article is part of the theme issue ‘The role of plasticity in phenotypic adaptation to rapid environmental change’.

1. Introduction

Phenotypic plasticity is the variation in phenotype produced by a single genotype in different environments. Along with adaptive evolution, plasticity is expected to play an important role in species’ responses to climate change, because each can alter the range of phenotypes expressed in a population as the environment changes. As a result, a growing body of empirical and theoretical literature seeks to understand the impact of each of these processes on demographic resilience to deteriorating environments [1–3]. Some progress has been made in our understanding of how plasticity and evolutionary change might individually affect resilience [3–6]. Much less is understood about the ways that evolutionary and plastic responses might interact with one another as populations respond to climate change.

Evolutionary rescue occurs when adaptive evolution allows a population to avoid extinction in a deteriorating environment [4,5]. Adaptive phenotypic plasticity can also ameliorate extinction risk by allowing a population to track closer to a changing optimum, increasing the likelihood of persistence [6–12]. The larger population sizes and longer persistence times facilitated by phenotypic plasticity may, in turn, enable evolutionary rescue by ‘buying time’ for adaptation to occur, and by increasing the likelihood of new beneficial mutations with larger effective population sizes [13]. However, if adaptive phenotypic plasticity increases a population’s fitness in the new environment, it will also tend to prevent evolutionary change by buffering against the effects of natural selection [14,15].

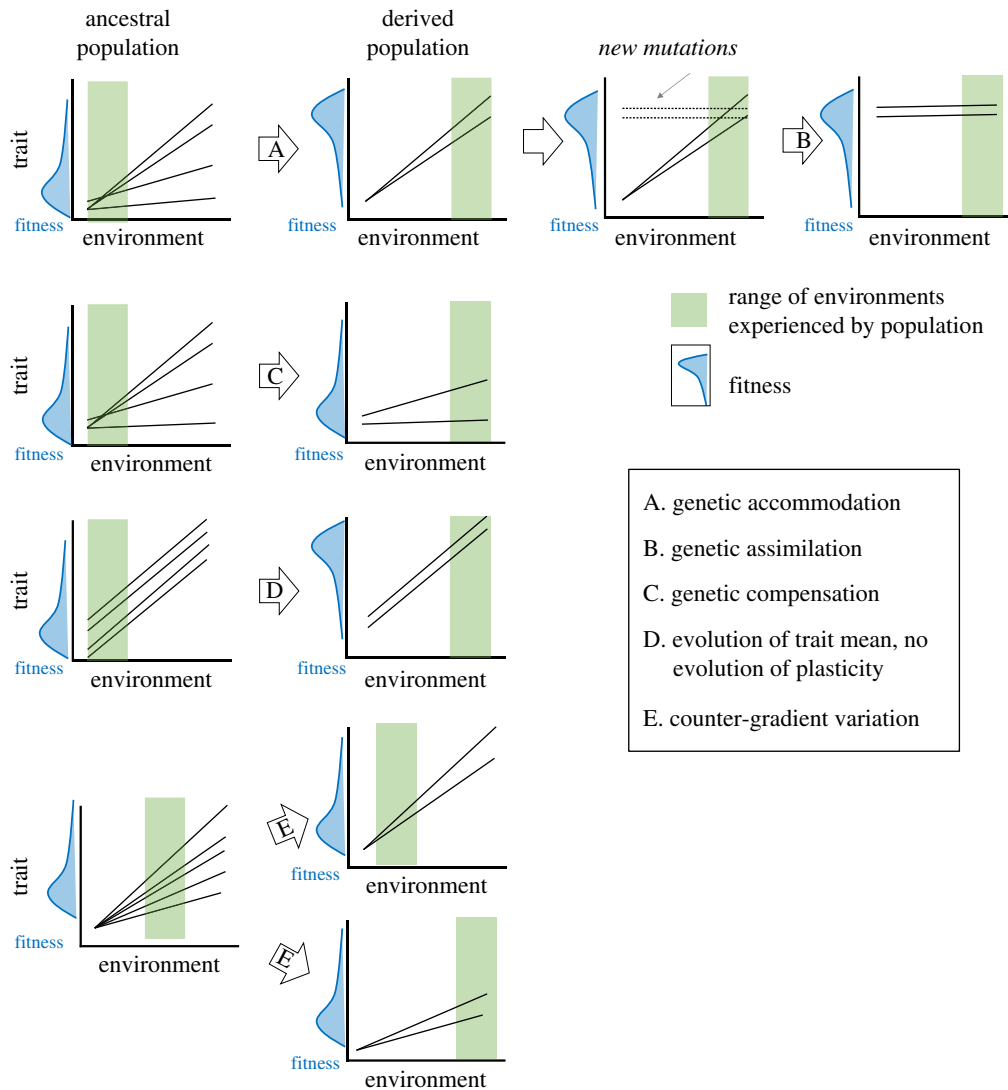


Figure 1. Evolutionary changes in phenotypic plasticity. Plots show hypothetical variation in reaction norms (the pattern of trait expression for a single genotype across a range of environments) before and after a shift in the environment, followed by natural selection. Boxes (green) indicate the range of environments experienced by a population, while lines along y axis (blue) denote the relationship between trait values and fitness for that population. (Online version in colour.)

As a further complication, plasticity itself may evolve [7,16,17]. Figure 1 shows possible patterns of genetic variation in plasticity, often depicted as a collection of reaction norms, each showing the relationship between variation in the environment and variation in the focal trait for a single genotype. Evolutionary changes in plasticity will depend on genetic variation in plasticity, changes in the environment and changes in optimal trait values. Possible evolutionary changes include increased plasticity if the most plastic genotypes bring phenotypes closest to the new optimum (genetic accommodation, figure 1A) [10,11,18,19]), followed by loss of plasticity if the new environment is stable (genetic assimilation, figure 1B) [10,20], or the loss of plasticity as an adaptation to resist phenotypic change in the new environment if plasticity is maladaptive (genetic compensation, figure 1C) [21–23].

Several recent theoretical works have considered the role of evolving plasticity in adaptive responses to climate change, showing that evolutionary changes in plasticity can contribute to the likelihood of persistence, but that its effects depend heavily on its costs [24]. These costs are typically included in models, but rarely measured empirically [25]. Evolving plasticity can also exacerbate the stochastic load imposed by an unpredictable environment, thereby reducing the probability of rescue [26]. And yet despite theory pointing to potential

positive and negative roles, the significance of evolving plasticity in the context of climate change responses remains an open question. This review will focus on the empirical evidence for evolving phenotypic plasticity in the context of climate adaptation, and what proportion of climate-driven evolutionary responses might be composed of changes in trait means versus changes in their environmental sensitivities (plasticity). If evolutionary changes in plasticity are an important component of evolutionary responses to climate change, it would imply that genetic variation in plastic responses to the environment ($G \times E$) could be an important predictor of vulnerabilities of species and populations to climate-driven decline or extinction.

It is important to note that not all human alterations result in a deteriorating environment from the perspective of the organism. Human activities are increasing the availability of a number of formerly limited resources, such as nitrogen and phosphorous, resulting in the relaxation of life-history trade-offs for many species [27]. Evolving plasticity is likely to play a key role in these cases too, as the genotypes with the greatest responsiveness to these newly available resources will be those most able to capture the available windfalls in increased fecundity, growth or longevity.

The idea that evolutionary changes in plasticity might tend to occur at the leading edge of trait evolution, the so-called

plasticity first hypothesis [28], is more than a century old [11]. It has been widely debated and is the subject of a substantial body of theory [14,15,18,19,22,26,24,28–31]. Although some of this theory makes generalized predictions, evidence for the role of plasticity in trait evolution varies substantially by trait type (e.g. morphology, physiology, life history) and taxonomic group, so that the empirical evidence should probably be considered separately in each context. Relative to other types of traits there is reason to believe that plasticity may already be especially high for the phenological and physiological traits that are likely to evolve in response to climate change. This is because climate change will entail alterations in the means, variances and predictabilities of environmental variables (temperature, moisture, carbon dioxide, pH) that already show substantial spatial and temporal heterogeneity in natural environments [32]. This heterogeneity occurs at temporal and spatial scales experienced by organisms within their lifespans, and is therefore expected to favour plasticity that maximizes fitness across environments [7,33,34]. Thus, plasticity already plays an important role in allowing organisms to maintain fitness across heterogeneous environments. A key question is whether sufficient genetic variation in plasticity ($G \times E$) exists to allow evolutionary changes in plasticity to contribute to the maintenance of fitness as patterns and scales of environmental heterogeneity change through time.

This question is difficult to address because direct observations of evolutionary responses to environmental change are relatively rare ([35] but see [36]), making it difficult to assess the relative contributions of changes in trait means versus changes in plasticity. However, there are also several proxies that can be used to understand the role of evolving plasticity: the first is local adaptation to environmental gradients across space (a ‘space for time’ substitution [37,38]). For example, if populations locally adapted to an environmental gradient in temperature are primarily diverged in their plastic responses to temperature, we might predict that evolutionary changes in plasticity would also be a key component of population responses to changes in temperature through time. Second, in short-lived organisms that are amenable to laboratory culture, experimental evolution studies can allow us to disentangle the relative contributions of changes in trait means versus changes in plasticity to evolutionary rescue. Third, genomic and transcriptomic data are increasingly allowing us to identify the genetic basis for adaptation. This provides another window into interactions between plasticity and adaptive evolution, because we can investigate whether loci that are environmentally responsive within populations are also disproportionately involved in population divergence through time or along environmental gradients.

2. Climate-driven evolution of plasticity: empirical examples

Two ways that evolutionary change in plasticity might contribute to evolutionary rescue in the context of climate change are alterations in responses to phenological cues, and alterations in the capacity for acclimation to abiotic variables, such as temperature, moisture or pH. Evolutionary responses to ongoing climate change in the wild are difficult to document, because the strongest evidence for adaptation comes from common garden experiments replicated through time, where genotypes from before and after climate-mediated selection are reared in a

controlled environment to disentangle genetic versus environmental effects on observed trait changes [2,35]. It is even more challenging to demonstrate evolutionary changes in plasticity over time because genotypes from the past and present must be reared across a range of environments to test for evolutionary changes in a trait’s environmental sensitivity.

One of the best cases for climate-driven evolution of environmental sensitivity comes from pitcher plant mosquitos *Wyeomyia smithii*. This species has a spring emergence time that is sensitive to photoperiod, and varies latitudinally. From 1972 to 1996, the photoperiodic response in this species shifted towards earlier emergence times across populations in the eastern USA from Georgia to Maine, a clear example of evolutionary change in the plastic response to photoperiod through time [39]. In fact, most if not all documented examples of climate-driven evolutionary changes in plasticity involve altered sensitivity to phenological cues, including changes in the migratory behaviour of European blackcaps (*Sylvia atricapilla*) [40], flowering time in sea beets (*Beta vulgaris* ssp. *maritima*) [41] and diapause timing in the fall webworm (*Hyphantria cunea*) [42]. Phenological mismatches are an important cause of climate-driven population declines [43,44], and therefore likely to be an important source of selection [45,46]. As a result, evolutionary changes in sensitivity to phenological cues will be an essential feature of evolutionary rescue (if it occurs) in many species [47]. However, not all observed evolutionary changes in phenology involve changes in environmental sensitivity. For example, in the field mustard *Brassica rapa*, another well-studied case of climate-driven evolution, there was no evidence for evolutionary change in environmental responsiveness, despite available genetic variation. In this species, there is an effect of drought on flowering time (E) and a genotype \times drought treatment interaction ($G \times E$) [48]. However, a selection event driven by a drought appears to have led to the evolution of decreased mean time to flowering (G), but no evolution of the responsiveness of flowering time to drought conditions ($G \times E$) [49,50].

Tests for evolutionary changes in plasticity over time are quite rare owing to the logistical hurdles listed above. However in species with resting eggs or seedbanks, a ‘resurrection ecology’ approach allows genotypes from the past and present to be tested in a common environment [51]. These species probably represent the best opportunity to test for evolutionary changes in plasticity through time, especially when combined with quantitative genetic ‘animal model’ analyses that allow environmental and genetic components of traits to be disentangled in datasets with imperfect pedigrees [52]. Finally, species with sufficient baseline trait data provide excellent opportunities to test for evolutionary change driven by extreme climatic events (e.g. [53]), supporting the urgent need for ongoing collection of both baseline data and living genome banks [54].

3. Population comparisons

In the absence of resources that allow researchers to document evolutionary changes through time, one way to understand how species are *likely* to adapt to environmental change is to measure evolved differences along current environmental gradients in space. Studies comparing locally adapted populations can ‘substitute space for time’ [37], measuring both the capacity for adaptation and the physiological mechanisms by which

adaptation occurs. This is one way to test for the relative importance of changes in trait means versus changes in plasticity: if local adaptation to environmental variables often occurs through changes in plasticity (shifts in reaction norm slopes), then we might also expect evolving plasticity to be an important part of population responses to changes in those same variables through time. On the other hand, if populations that are locally adapted to an environmental variable diverge primarily in trait means, rather than reaction norm slopes, this would suggest that evolutionary changes in plasticity are less likely to make an important contribution to adaptation.

One of the most common ways for populations along latitudinal gradients to differ in the slopes of their reaction norms is counter-gradient variation in the sensitivity of metabolic rate and development time to temperature, as depicted in figure 1E [55]. This is extremely common in temperate ectotherms, including fish (reviewed in [56]), marine invertebrates (reviewed in [57]), insects (reviewed in [58]) and amphibians (reviewed in [59]). Thus, to the extent that adaptation to climate change mirrors local adaptation to temperature, the ubiquity of latitudinal variation in the temperature sensitivity of biological rates suggests that evolutionary change in temperature sensitivity of metabolism and development will also be an important component of evolutionary responses to a changing climate.

It is also common for populations of temperate plants and ectotherms along latitudinal and altitudinal gradients to vary in responses to phenological cues [60], with strong selection on loci contributing to divergence in phenological timing [61] and rapid establishment of latitudinal clines in phenology in introduced species [62]. A recent common garden experiment transplanted replicate genotypes of the riparian tree *Populus fremontii* across 5° of latitude, demonstrating that populations varied in their phenological plasticity and had substantial within-population G × E [63]. Interestingly, fitness effects of plasticity varied by trait and environment, with both adaptive and maladaptive trait changes. However, in all cases, the presence of G × E and a strong correlation with fitness predict evolutionary changes in phenological plasticity in response to changing climates in this species. These patterns suggest that, as has already been observed, changes in sensitivity to phenological cues will play a key role in evolutionary responses to climate change, especially in organisms with distinct life-history stages and strong links between fitness and the timing of life-history transitions.

Other traits show more mixed evidence for latitudinal variation in plasticity. For example, studies of upper and lower thermal limits have shown parallel reaction norms in *Tigriopus* copepods [64], *Drosophila* [65,66] and *Anolis* [67] (although not for *Arabidopsis* [68]). To the extent that reaction norms for thermal limits are more likely to be parallel across latitude, these studies suggest that evolutionary change in thermal tolerances might be more likely to occur through evolutionary changes in trait means rather than their reaction norms, as illustrated in figure 1D.

Moving beyond macroscopic traits, another way to test for among-population variation in plasticity is via comparative transcriptomics [69]. In these studies, the expression level of each gene can be considered a phenotype. As a result, comparing gene expression responses to environmental conditions among populations represents an opportunity for a fine-scaled examination of how the environmental responsiveness of phenotypes diverges among populations. A substantial number of studies have made this comparison, especially in the context

of populations that vary in their sensitivity to thermal stress [70]. In some cases differential gene expression between the stress and control treatments is greater in the more tolerant population, as depicted in figure 1A (whitefly, *Bemisia tabaci* [71], seagrass *Zostera marina* [72], trout *Oncorhynchus mykiss* and *Salmo trutta* [73,74], stickleback *Gasterosteus aculeatus* [75], *Panicum* grass [76]). In other studies, the sensitive population had greater differential gene expression between treatments (copepod, *Tigriopus californicus* [77], coral *Acropora hyacinthus* [78], snail *Chlorostoma funebris* [79]). Still other studies have shown largely parallel reaction norms between divergent populations, as depicted in figure 1D (*Drosophila* [65,66], *Anolis* [67]). However, on the whole, it appears to be more common that populations with divergent environmental tolerances show divergent gene expression responses to the relevant environmental variable, supporting the hypothesis that divergence in the plasticity of environmentally responsive gene expression is an important component of stress adaptation.

A final comparative test for climate-driven evolution of plasticity comes from contrasts between the native and novel ranges of invasive species. Meta-analyses suggest that plasticity might facilitate invasions, because at the species level, invasive species appear to have greater plasticity than non-invasive species ([80], but see [81]). However, a growing number of studies also suggest that plastic traits may evolve during invasions, so that invasions may be facilitated not only by plasticity, but evolutionary changes in plasticity. For example in the Great Lakes, a comparison between two fish that were introduced at similar times but differed in the geographical extent of their invasions revealed much greater transcriptional plasticity in response to temperature on the part of the more successful invader [82] with genes involved in the thermal response showing a signature of selection in the invaded range [83]. Thermal plasticity has also evolved in small cabbage white butterflies (*Pieris rapae*), with introduced populations exhibiting divergent thermal reaction norms for adult body size [84], and in the temperature sensitivity of development in wall lizards (*Podarcis muralis*) introduced to England from southern and western Europe [85]. A comparison of embryonic transcriptomes in this species between native and invaded populations revealed divergence in gene expression that was enriched for genes that are responsive to temperature in the native populations, however in this case, the evolutionary change was in the baseline expression in the invaded range, rather than its temperature sensitivity, consistent with the pattern shown in figure 1D. Invasive populations have also shown evolved differences in their responsiveness to phenological cues, including flowering time in an invasive grass [86], diapause timing in fall webworms *Hyphantria cunea* [87], and photoperiodic response of the Asian tiger mosquito *Aedes albopictus* [88].

Taken together, divergence in reaction norms among locally adapted populations and between native and invasive populations suggests that it is extremely common for populations to adapt to climatic conditions through divergence in their plastic responses to environmental variables. However, there is also a notable lack of consistency in the direction of divergence—sometimes the derived or the more stress tolerant population exhibits greater plasticity, and sometimes it exhibits less. Theory suggests that these apparently conflicting results might be driven by the amount of time since colonization: a shift in the environment will initially select for increased plasticity (accommodation) followed by evolution of decreased plasticity in the new environment, if it is stable (assimilation),

as depicted in figure 1A,B [89]. Experimental evolution (discussed below) may help to disentangle the predicted effects of selection on phenotypic plasticity over different time scales.

4. Laboratory experiments

In some short-lived organisms, predictions from evolutionary theory can be tested in the laboratory via controlled experiments. Relatively few experiments have directly tested interactions between plasticity and adaptive evolution during evolutionary rescue [90,91], however, we can still gain insight from the many others that have selected for changes in trait means in a single environment and observed changes in plasticity as a correlated response to selection. Most of these have observed that directional selection on trait means resulted in increased plasticity (reviewed in [92,93]), consistent with predictions from theory [19] and the pattern shown in figure 1A. However, others have observed decreased plasticity as a correlated response to directional selection on trait means, including a decrease in plasticity of heat tolerance in nematodes and copepods [94,95] and a decrease in the plastic response to CO₂ in *Bromus* grass following evolutionary adaptation to atmospheric CO₂ enrichment [96], consistent with the pattern shown in figure 1B. Interestingly, all three of the latter examples involve physiological tolerances, while many of the studies reviewed previously [92,93] involved morphological traits, which are less labile and more likely to be fixed during development [97]. This points to potentially different responses among types of traits under selection.

Ultimately the effects of directional selection on plasticity depend on reaction norm parameters [98], so that directional selection could lead to either increased or decreased plasticity, depending on the sign of the correlation between trait means and reaction norm slopes [99]. Novel environments have not (by definition) played an important role in selection on existing reaction norms, so whether or not plasticity tends to be adaptive in the new environment will depend heavily on cross-environment correlations for fitness and whether genotypes that have high fitness in future environments also have high fitness in current ones [100]. As a further complication, organismal phenotypes often do not respond linearly to environmental change. For example, if some parts of the temperature range (e.g. freezing) are more consequential as environmental cues or physiological tipping points, small changes in temperature may produce larger than expected changes in organismal phenotypes, especially when they fall outside the range of environments previously experienced in that population [101,102].

5. Genomic data

If adaptation to climate change occurs through modification of plastic responses, we can expect divergence to target environmentally responsive genes. In particular, adaptation should alter the expression plasticity of environmentally responsive transcripts, reflected in an increased divergence between populations for regulatory regions of genes involved in plastic environmental responses within populations [103].

Overlap between plastic and evolved responses appears to be relatively common in comparative transcriptomics studies, especially those measuring responses to variation in temperature. A comparison between heat-tolerant and heat-sensitive populations of the coral *A. hyacinthus* found that 60 genes

upregulated under temperature stress in the heat-sensitive corals had a reduced response in the heat-tolerant corals [78]. These same genes also had higher baseline expression in the heat-tolerant compared to heat-sensitive corals under ambient conditions, a phenomenon referred to by the authors as ‘front-loading,’ consistent with genetic assimilation shown in figure 1B. This same pattern of higher baseline expression plus lower expression plasticity in the more tolerant population was also observed in *Porites astreoides* corals [104], *Chlorostoma funebalis* snails [105] and *Zostera marina* seagrass [72]. The higher baseline expression of environmentally responsive genes noted in these studies might represent an evolved response to a frequently encountered stress, allowing these populations to maintain tolerance in the absence of an acclimatization response. Overlaps between the genetic basis of plasticity and population divergence have also been observed in European fire salamanders, *Salamandra salamandra* [106], grayling *Thymallus thymallus* [107] and wall lizards *P. muralis* [85].

Genomic scans for outlier loci can also be used to test for an overlap between plastic and adaptive divergence by investigating whether genes differentially regulated in the response to an environmental variable also show heightened divergence in regulatory regions for populations that are locally adapted to that same variable. In particular, *cis*-regulatory variants might create or disrupt transcription factor binding sites, altering the environmental sensitivity of gene expression [108]. Alterations to transcription factors may also alter their binding affinity, or even render them inactive, thereby blocking expression of relevant pathways. In *Mimulus guttatus*, a reciprocal transplant revealed that genes with elevated divergence in promoter regions between populations were also disproportionately more likely to be differentially expressed between habitats [109]. In *Arabidopsis*, genes with variable responses to drought and cold stress ($G \times E$ for gene expression) were disproportionately correlated with climate variables in population comparisons, relative to other genomic regions and also had greater polymorphism in promoter regions [110].

Trans-regulatory mutations also contribute to climate adaptation, as in the CBF locus in *Arabidopsis*, which comprises three transcription factors that are induced by low temperature, and regulate a set of genes that impart freezing tolerance. In a warm-adapted population, the regulatory response to low temperature is dampened owing to a mutation that renders one of the three proteins (CBF2) non-functional [111]. This altered regulatory response contributes to the lower freezing tolerance of warm-adapted populations. A survey of 477 wild accessions indicated that that CBF sequence variation is strongly associated with winter temperature, and that disruption of CBF function is involved in multiple parallel adaptive transitions to warmer climates [112]. In this case, adaptation appears to have occurred through genetic compensation—the dampening of a plastic response that was no longer favoured in the novel environment, illustrated by the response in figure 1D.

Divergence in environmentally responsive gene expression is also observed in stickleback, where genes that responded differentially to temperature between marine and freshwater populations were located within outlier regions of genetic divergence, previously implicated in local adaptation [75,113]. Greater upregulation of HSPB1 in more thermally tolerant population of *Tigriopus* copepods was also tied to *cis*-regulatory divergence [114], and a whole genome scan of *B. rapa* before and after a climate (drought)-driven selection event identified Fst outliers related to regulation of drought responses and

flowering time [115]. The contribution of environmentally responsive gene regulation to local adaptation even appears to be repeatable over deep evolutionary time: two distantly related pine species separated by more than 140 million years had high overlap in the genes involved in local adaptation, and these genes were disproportionately involved in phenology and responses to climate stress [116].

6. Genetic variation in plasticity ($G \times E$)

Evolution depends on genetic variation, and so the extent to which populations will respond to climate change through evolutionary adjustments in plasticity will depend heavily on genetic variation for environmental responsiveness of climate-related traits ($G \times E$). However, the magnitude of genetic variation for slopes and curvatures of reaction norms varies greatly by taxon and trait [117], so a key question is what factors tend to maintain genetic variation for plasticity within and between natural populations, and why these factors might vary across traits and species.

Saltz *et al.* [118] review examples of $G \times E$ estimates in natural populations and lay out several hypotheses for factors expected to maintain high levels of $G \times E$. These include factors that tend to maintain genetic variation more generally, including large effective population size, high mutation rate, spatially varying selection and relaxed selection. From this perspective, the variation in reaction norm shapes driven by spatially varying selection and local adaptation to environmental gradients reviewed above are not just a window into mechanisms of future adaptation, but also a source of variation on which natural selection can act.

Given that mutation rate is key to maintaining variation, another important empirical question is whether reaction norm slopes tend to have large or small mutational target sizes [118]. It has been argued, for instance, that there should be more available mutations to modify plasticity, because modifications to plasticity involve tweaks to the expression of a pre-existing trait, rather than the origin of a new gene or the modification of a potentially conserved protein [119]. Furthermore, *trans* effects on gene expression have a potentially large mutational target size if there are many transcription factors affecting the expression of a single gene.

It is also possible that highly environmentally responsive traits will tend to exhibit more genetic variation, including variation in responsiveness $G \times E$ [118,120]. This is supported by the many examples (reviewed above) indicating that genes that are environmentally responsive within populations are disproportionately involved in population divergence, the product of selection on past $G \times E$ within populations. If magnitude of plasticity correlates with genetic variation in plasticity, this would imply that the factors that favour plasticity (e.g. heterogeneous environments and predictable cues) would also tend to maintain $G \times E$. Crucially, plasticity depends on the existence of mechanisms to sense and respond to the environment. Both of these may either fail to evolve or secondarily be lost in organisms from highly stable environments, as in the extreme case of the missing heat shock responses in Antarctic notothenoid fishes [121]. Especially in these extreme cases of highly stable environments, *variation* in responsiveness to the environment is unlikely to accumulate easily when the magnitude of such responsiveness is already low. As a result, species from stable environments will be doubly vulnerable to climate

change—they are more likely to have narrow ranges of environmental tolerance, but also to have less genetic variation in tolerance, making them less likely to evolve wider tolerances over time relative to their eurythermic counterparts.

D.H. Janzen famously argued that ‘Mountain passes are higher in the tropics,’ [122, p. 233], by which he meant that muted seasonal temperature fluctuations at tropical (as compared to temperate) latitudes would maintain comparatively narrower ranges of environmental tolerance in tropical species. As a result, environmental change along altitudinal gradients in the tropics would comprise comparatively more turnovers in species’ environmental niches. If the magnitude of physiological plasticity tends to correlate with the magnitude of genetic variation in plasticity, this would imply an evolutionary corollary to Janzen’s observation: organisms from more stable environments will not only have muted plasticity, but also diminished capacity to evolve increased plasticity over time, resulting in less labile environmental tolerance limits and decreased abilities to move up and down Janzen’s mountains over evolutionary time.

Even in more heterogeneous environments, $G \times E$ within populations can also be extremely limited if reaction norm slopes are under strong selection [100,123]. On the other hand, if $G \times E$ is limited by strong selection, we might still expect genetic variation for plasticity in novel environments, where trait expression has not experienced strong prior selection for canalization [124].

Finally, ‘niche-constructing traits’ can alter the environments experienced by different individuals, with a resultant increase in environmental heterogeneity experienced by the population, and an increase in the probability that variation in other environmentally responsive traits will be maintained [118,125]. Thus, in the context of climate warming, species with variation in thermoregulatory behaviour (e.g. [126,127]) can be expected to maintain greater variation in thermal reaction norms. Genetic variation in phenology (e.g. [128,129]) can also be considered a form of variation in niche construction, because the timing of reproduction influences the offspring’s environment. As a result, genetic variation in phenology provides fodder for adaptive responses to climate change, but could also serve to maintain genetic variation in physiological reaction norms, another pool of targets for selection.

7. Conclusion, implications and future directions

Climate change will alter environmental parameters that already vary over temporal and spatial scales experienced by individual organisms. This implies that over evolutionary time, natural selection may act on variation in physiological mechanisms that organisms already use to tolerate environmental variation, providing a direct link between current physiological plasticity and longer-term evolutionary adaptation to climate change. Evidence for this link comes from studies of local adaptation, where the genetic basis for adaptive physiological differences between populations along environmental gradients often mirrors the mechanistic basis for physiological responses to those same variables within populations.

If local adaptation provides a preview of future adaptation to climate change, available data on plastic and evolutionary responses to current environmental gradients suggest several insights. First, some traits are more likely to

diverge in their environmental responsiveness than others. In particular, it is common for populations along environmental gradients in temperature to differ in their sensitivity to phenological cues, and in the temperature dependence of metabolic rates. This suggests that these two types of traits may be especially likely to exhibit evolutionary changes in plasticity in a warming climate. Second, genetic variation for plasticity ($G \times E$) varies by trait type and by species, with $G \times E$ likely to be correlated both with effective population size and degree of environmental heterogeneity. The capacity for phenologically and physiologically plastic responses to environmental heterogeneity is strongly tied to extinction risk from climate change [3,43,44,130]. Therefore, if genetic variation in plasticity is correlated with both the magnitude of plastic responses and with effective population sizes, we might expect a 'rich get richer' scenario in the context of climate change vulnerability: species with larger effective population sizes will be demographically less vulnerable to climate change, and will also possess more genetic variation, thereby facilitating trait evolution and the potential for evolutionary rescue. Species with greater adaptive plasticity may avoid population decline by tracking closer to the new phenotypic optimum, but may also possess greater genetic variation for plasticity, increasing the likelihood that natural selection can fine-tune the plastic response over time.

It is important to note that plasticity can also be maladaptive, especially if cues eliciting the plastic response become less reliable as the environment deteriorates. Here, too, genetic variation in plasticity may be key to adaptive responses to climate change, as only populations with genetic variation in plasticity can begin to purge the most maladaptive responses.

Comparisons between locally adapted populations strongly suggest that evolution of environmental responsiveness plays a key role in adaptation to climatic gradients in space, pointing to the potentially important role of evolving plasticity in adaptation to changing environments through time. However, theory also suggests that evolving plasticity can exacerbate the stochastic load imposed by an unpredictable environment, thereby reducing the probability of evolutionary rescue [26]. This highlights a key limitation of the 'space for time' substitution: comparisons between populations will not show us the cases where evolutionary changes in plasticity prevented environmental adaptation, because we cannot compare populations that failed to colonize a new environment and therefore do not exist. Thus, population comparisons point to a potentially central role for evolving plasticity in climate adaptation, but the most important question, whether evolving plasticity more often facilitates or impedes evolutionary rescue, remains unresolved. Two future research directions would help to address this issue:

1) **Experimental evolution.** A key unresolved question is whether greater genetic variation for plasticity tends to increase the probability of rescue. This could be addressed in experimental studies comparing rates of adaptation to

changing environments in populations that differed in levels of genetic variation for plasticity ($G \times E$). Ideally, such experiments would test the effects of $G \times E$ on probability of rescue in different contexts, including fluctuating environments, and in environments that varied in the predictability of their cues. Because comparatively more studies select for changes in trait means in a single environment, another piece of 'low hanging fruit' is to add measurements of plasticity to these experiments, to test whether selection on trait means often results in correlated changes in plasticity [93]. Mutation accumulation experiments in micro-organisms can also be used to ask whether genetic variation in plasticity accumulates more easily in some traits than in others, for instance, in the expression of genes that have a larger mutational target size because they are controlled by a larger number of transcription factors.

Microorganisms possess some traits (experimental tractability, short generation times) that render them ideal for experimental evolution. However, on the other hand, there are other features of microorganisms (e.g. asexual reproduction, large effective population sizes) that will limit the applicability of these findings to other species. Therefore, researchers must try to balance experimental tractability with applicability when choosing the appropriate system to test these questions via experimental evolution.

2) **Comparative studies.** The comparisons among locally adapted populations reviewed here highlight the potential role of evolving plasticity in climate adaptation. But comparative studies of invasive species can also be used to address the larger question of whether evolving plasticity contributes to evolutionary rescue, because researchers can compare closely related species that vary in their invasiveness to ask whether more successful invaders tend to have greater genetic variation for plasticity, and whether plasticity tends to evolve in the new range, relative to the old one. Comparative studies among closely related species could also be used to investigate factors that tend to maintain genetic variation for plasticity—for instance, whether $G \times E$ is higher in species and populations with greater plasticity, or in traits or portions of reaction norms under relaxed selection. Many of the factors that contribute to evolutionary dynamics in real populations cannot be captured in the lab, and as a result comparative studies continue to represent one of the best opportunities to understand evolutionary adaptation to changing environments.

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