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Review

The Potential for Rapid Evolution under Anthropogenic Climate Change

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Understanding how natural populations will respond to rapid anthropogenic climate change is one of the greatest challenges for ecologists and evolutionary biologists. Much research has focussed on whether physiological traits can evolve quickly enough under rapidly increasing temperatures. While the simple Breeder's equation helps to understand how extreme temperatures and genetic variation might drive within-population evolution under climate change, it does not consider two key areas: how different forms of phenotypic plasticity interact and variation among populations. Plasticity can modify the exposure to climatic extremes and the strength of selection from those extremes, while differences among populations provide adaptive diversity not apparent within them. Here, we focus on terrestrial vertebrates and, with a case study on a tropical lizard, demonstrate the complex interplay between spatial, genetic and plastic contributions to variation in climate-relevant physiological traits. We identify several problems that need to be better understood: which traits are under selection in a changing climate; the different forms of plasticity relevant to population persistence and rapid evolution; plastic *versus* genetic contributions to geographic variation in climate-associated traits and whether plasticity can be harnessed to promote persistence of species. Given ongoing uncertainties around whether natural populations can evolve rapidly enough to persist, we advocate the use of field trials aimed at increasing rates of adaptation, especially in systems known to be strongly impacted by human-driven changes in climate.

Introduction

It is now well established that emissions from human activities are causing rapid climate shifts, and changes in both the mean and variability of temperature and rainfall are apparent [1]. These changes are already having observable effects on biodiversity, including on the distributions and phenotypes of species as well as on the composition of biological communities [2,3]. Though some species will benefit, various modelling studies have predicted catastrophic outcomes for biodiversity overall [4,5], even though many taxa have proven resilient to climate changes (in non-modified habitats) over recent geological history [6]. These modelling projections include large-scale changes, such as the loss of more than half of a species' range for 49% of all insect species, 44% of plants, and 26% of vertebrates [5]. They also predict large-scale changes in ecosystems, for instance in South America, where many rainforests may turn into savanna or grasslands [4].

Species can survive rapid climate change through several processes [7,8] — they could be relatively unaffected if the new conditions are well within their tolerances and changes to biotic interactions do not impact them [9], if their geographic ranges shift to track climate [10], or if they are able to adapt to climate change in their current range [11]. Thus, depending on the levels of exposure and their capacity to adapt, species may be winners that are able to occupy and even thrive in old and new habitats, or losers that are unable to thrive in available habitat and risk extinction. For organisms with low dispersal abilities, or for more mobile species in strongly fragmented habitats, rapid adaptation will often be critical for survival.

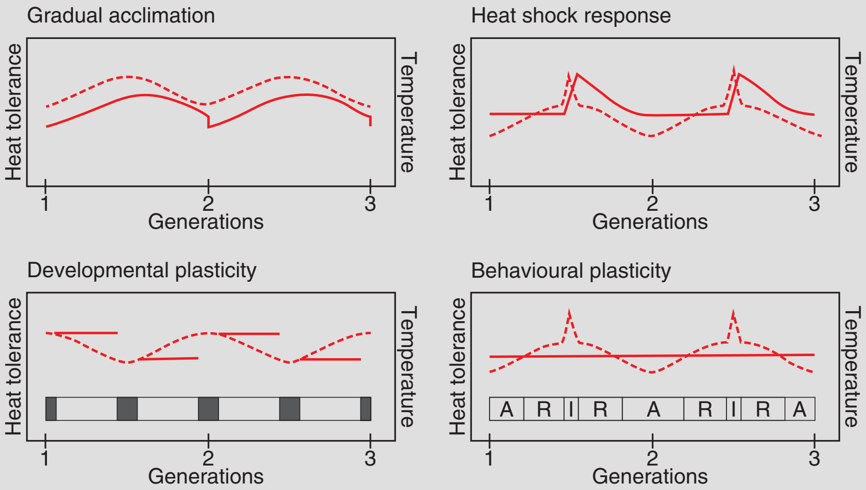
Here, we focus on the potential for the rapid adaptive evolution of terrestrial animals to prevent extinction [12–15]. This is often referred to as 'evolutionary rescue' [16,17] and is most likely to work for species with relatively short generation times and large populations, which can mount effective evolutionary responses to climate change. Comparisons of populations or species over the period of rapid warming from the mid 20th century to now have revealed many examples of shifts in climate-related phenotypes, especially their phenology [18]. In principle, such changes could be due to phenotypic or behavioural plasticity, genetic evolution or a mix of both. Most evidence so far points to plasticity (Box 1) [15,19,20], but few studies have directly tested the genetic basis of such shifts in climate-related phenotypes over time. The evidence to date—from resurrection experiments [21] and longitudinal studies [22–25] — indicates genetically-based shifts in response to climate, but also complex interactions between evolutionary and plastic responses. The complexity of possible responses, as well as the very speed of climate change, make predictions difficult.

Understanding and predicting the capacity for rapid evolution in response to climate change is a very active area of research on natural populations and model systems [16,26,27]. There is also growing interest in combining estimates of evolutionary potential

Box 1. Forms of phenotypic plasticity.

Phenotypic plasticity is expressed in different ways, each of which may use different biochemical pathways within an organism and thus may evolve separately. Reversible responses to environmental change can take place gradually or in response to acute environmental change within a single generation. Gradual acclimation is the continuous shift of traits (*e.g.*, critical thermal maximum, CT_{max}) in response to a changed environment in the laboratory or across seasons [82]. A heat shock response is the abrupt shift (often minutes or hours) of the trait in response to an extreme event, also referred to as 'hardening'.

Developmental plasticity is the capacity of the same genotype to produce different phenotypes in response to conditions during development [112], and is generally considered non-reversible. In the context of thermal limits, it refers to traits such as CT_{max} being set for the lifetime of the individual based on conditions experienced prior to maturity or hatching [113]. Behavioural plasticity refers to the ability of mobile organisms to regulate their environment. For individuals in thermally stressful environments, thermoregulation occurs through the choice of optimal or less stressful microhabitats, and/or through periods of inactivity during stressful conditions [54].



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Different forms of plasticity.

Illustration of how environmental variation and different forms of plasticity would affect a tolerance trait (solid lines) affected by temperature (dashed lines) in a population with annual seasonal variation and non-overlapping generations. (Upper left) Gradual and reversible acclimation. (Upper right) Transient heat shock responses. (Bottom left) Effect of developmental plasticity, where generation time is less than one year to illustrate effect of development under different thermal conditions. The boxes in the bottom left panel show development time (grey) and the period as mature individuals (white). In the bottom right panel where individuals behaviourally moderate activity to prevent heat stress, letters refer to periods of high activity (A), restricted activity (R), and inactivity (I).

into spatial modelling of species' persistence under climate change [28,29]. However, the current human-driven environmental change requires adaptation at a rate that is experimentally untested in the vast majority of terrestrial organisms. As such, there is only a rudimentary knowledge of how adaptation will occur for the vast majority of species. There are many traits that are relevant to fitness in a changing climate — including phenological, morphological, life-history and physiological traits. In particular, traits associated with heat tolerance can include shifts in breeding time, body size, or thermal performance. Thermal performance, as relevant to climate extremes, is measured in a variety of ways, including thermal performance curves, lethal temperatures, heat knockdown times and survivorship [30].

In this review, we mostly restrict our attention to just two traits: heat tolerance and desiccation resistance. These are commonly-measured physiological traits because the most obvious challenges to life over coming years will be increasing maximum temperatures, as well as heatwaves, and, in some places, also decreasing rainfall and severe droughts. We also largely restrict our discussion of empirical examples to terrestrial ectotherms, because these are the most extensively studied group with regard to these traits. Across all taxa and ecosystems, however, population responses, including rapid evolution, will take place under a press–pulse framework; the continuous press of changing climate, accompanied by irregular pulses of even more extreme temperature [31], and so we adopt this backdrop as our starting point.

Below, we lay out the fundamentals of rapid evolutionary change and then delve into how plasticity and genetic evolution interact to determine evolutionary change within and among populations (Figure 1). Local adaptation and often ubiquitous geographic variation in climate may result in substantial variation in climate-relevant traits among populations. Given likely constraints on within-population evolution, locally adapted populations could be a key resource for managing species in the age of rapid climate change.

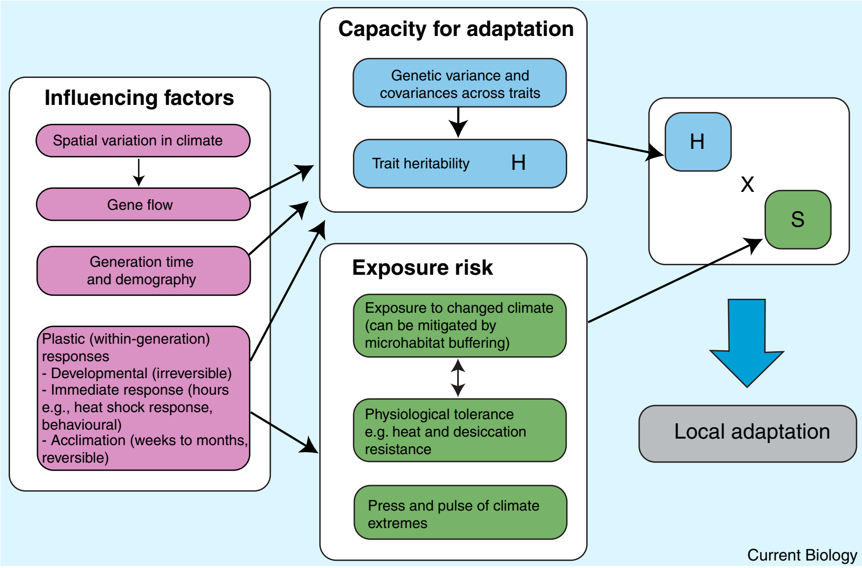


Figure 1. Process of local adaptation.
Factors and processes that affect the capacity of populations and species to evolve in response to rapid climate change. This illustrates the complex interplay of ecological and organism-specific variables that influence the ability of local populations to adapt.

Rapid Evolution within Populations

In the right conditions, adaptation can happen very rapidly. Where there is existing genetic variation for a trait within a population, and that trait comes under strong selection, the trait can change substantially across just a few generations. This potential is described by the breeder's equation, which states that the phenotypic response to selection (R) is equal to the heritability of the trait (h^2) multiplied by strength of selection (S): $R = h^2S$. The breeder's equation is a simplification and — for various reasons — is rarely met in nature [32], but it is a useful thought tool. It immediately shows that adaptation can happen quickly but is limited by genetic variation for the trait (heritability) and by the strength of selection. In practice, genetic co-variance between multiple traits under selection may cause the response to be smaller than if only a single trait was under selection [33,34]. This happens because, unless the direction of selection is perfectly aligned with the direction of trait covariation, that covariation effectively reduces the amount of total trait variation available for selection to act upon [34]. Rapid adaptation in nature is also limited by population viability, where increased mortality or decreased reproduction accompanying selection can cause populations to decline and perhaps go extinct before they adapt (Figure 2A,B) [17]. Nonetheless, by measuring selection and trait heritability we can get a sense of the evolutionary pressure on climate-relevant physiological traits as well as their 'best-case' capacity to adapt in response to that pressure.

Selection

Direct evidence for selection via differential mortality during climatic extremes is commonplace. For example, hurricanes have been observed to kill animals ranging from anole lizards to sparrows non-randomly with regard to body size and limb length, resulting in population-level shifts in trait means [35,36]. Thus, we might reasonably expect such dramatic, pulse events to exert selection on physiological traits that mediate exposure. We might also expect much less dramatic selection (affecting fecundity rather than survival) to be ubiquitous, driving adaptation to particular local conditions. Indeed, as interest in climate-driven evolution increases, there is a growing list of studies demonstrating selection on thermal performance metrics in response to climatic conditions [37,38].

While there is now some evidence from natural populations that selection acts directly on physiology, it is important to appreciate that changing climatic conditions do not necessarily imply selection. To understand why, we can take the example of an organism's desiccation resistance, the rate at which it loses water, which varies across individuals in a population. Imagine the driest month of the decade; four possibilities follow: first, all individuals survive, fitness is uniform (survival = 1), and there is no selection on desiccation resistance; second, all individuals die—again, fitness is uniform (survival = 0) and there is no selection on desiccation resistance; third, some individuals are killed by lack of water but because they chose poor shelter sites. Here, fitness varies, but in a way that is uncorrelated with desiccation resistance, so again, no selection on desiccation resistance. Finally, we have the possibility that an organism's trait value for desiccation resistance affects the probability that it lives or dies; it is only in this final situation that we see selection on desiccation resistance.

These four possibilities are important because it is not always clear that the traits measured are under selection in a changing climate. For example, it is often assumed that species occupying a small geographic and climatic range also have narrow physiological tolerances and thus are highly susceptible to extinction under climate change. But many narrowly distributed species have thermal tolerances well beyond those required within their current distribution [9,39]. As a consequence, there may often be little direct selection on physiological traits as such species experience climatic extremes or shifts.

Genetic Variation

When a trait of interest is under selection, the response to selection is determined by the trait's heritability — the proportion of the population's total phenotypic variation that is due to genetic variation that is additive across alleles and loci. Estimating trait heritability is a formidable challenge and is most often achieved in model organisms. A recent meta-analysis of experimental estimates of heritability of heat tolerance (specifically, critical thermal maximum, CT_{max}) in insects (mostly *Drosophila* species) reported moderate values ($h^2 < 0.3$), with higher heritability in environments with greater temperature variability [40]. All else being equal, this implies greater potential for rapid evolution at higher latitudes, where there is also greater temperature variability and where warming is expected to be greatest. Efforts

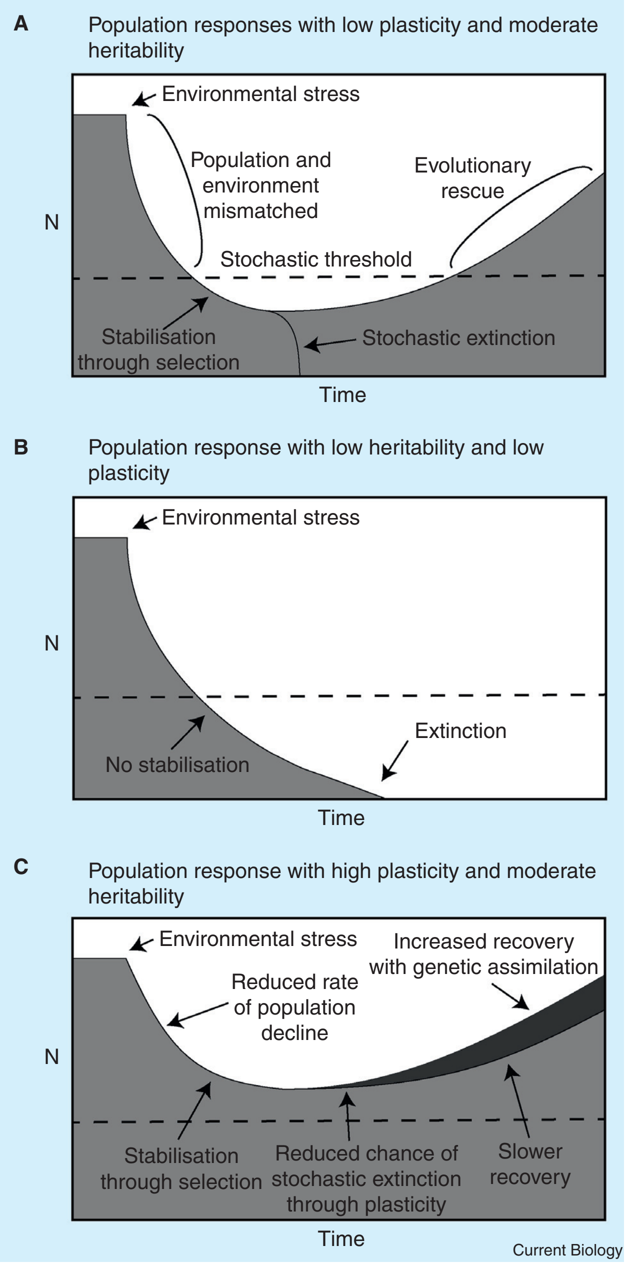


Figure 2. Population responses to environmental stress.
Possible responses of a closed population over time in response to a step-change in the environment (modified from [17]). (A) Populations with little ability to mount a plastic response and moderate heritability for a key trait are initially stabilized through selection. Likely outcomes include evolutionary rescue through genetic adaptation, or stochastic extinction if the population has fallen below the stochastic threshold. (B) The continued decline toward extinction of a population that lacks both heritable trait variation and capacity for a plastic response. (C) Populations with high plasticity and moderate heritability decline more slowly due to (adaptive) plastic responses, reducing the risk of stochastic extinction. Plasticity may also slow the rate of evolutionary rescue, unless there is genetic assimilation of phenotypes generated by plasticity.

are increasing to measure heritability in non-model species, and these are yielding similar results: variable, but generally moderate to low heritability [41]. Although most traits in most species are heritable to some degree, desiccation resistance (a key physiological trait) showed no response to selection under extreme conditions in two species of rainforest fruit fly, whereas other traits showed more typical levels of response to selection [42]. In contrast, the same populations were found to have moderate levels of heritability and selection response when subject to less severe (and more realistic) dry conditions [43]. This example reminds us that, as for heat resistance [40], the conditions and methods under which heritability is measured often affect the estimate.

One powerful theoretical expectation is that the heritability of total fitness should be very close to zero [44]. Traits strongly linked to fitness will have low heritability because they are under such strong selection that additive genetic variation is reduced by sustained selection. In the context of climate change, this expectation has several important corollaries: first, observations of low heritability of climate-relevant traits (primarily from studies on insects) could indicate strong and sustained selection, pointing to the importance of these traits to fitness; second, we would expect the heritability of climate-relevant traits to vary depending on whether or not a population is at a climatically-determined (*versus* biotically-determined) range margin. Certainly, the few studies comparing relative heritability of thermal traits among populations generally support lower heritability in stressed populations [45]; finally, if populations are under strong and spatially variable selection, we might expect much of the genetic variation for climate-relevant traits to be present between, rather than within, populations.

Possibly the most important complexity missed by the basic breeder's equation is that selection operates on whole organisms, not individual traits; this means that fitness is inherently multivariate. While it is convenient to think of a single organismal trait (*e.g.*, CT_{max}), the reality is that the survival of individuals with a given value for one trait depends also on many other traits, for example optimal performance temperature (T_{opt}), critical thermal minimum (CT_{min}), desiccation resistance, body size, sex or thermal breadth. To the extent that these fitness-related traits are genetically correlated (*e.g.*, through genetic pleiotropy or linkage), or are under parallel or opposing selection, evolutionary response for the focal trait will be enhanced or retarded. Such genetic correlations are not unusual, and can also vary in sign (*e.g.*, negative for body size and CT_{max} in some species, but positive in others [46–48]). The outcome of selection for desiccation resistance over seven generations in the fly *Anastrepha ludens*, for example, illustrates the complexities of selection in multivariate space: here, selection on desiccation led to increases in lifespan, body size and age of first reproduction, while it reduced egg production and prolonged the pupal stage [26].

Such limits imposed by multivariate trait structure may explain the strong phylogenetic inertia observed in CT_{max}. This trait appears strongly phylogenetically constrained, particularly in its upper limit, across a range of taxa [39,49]. By contrast, evolutionary inertia does not appear to apply as strongly to traits such as CT_{min} or desiccation resistance [50]. The proximate cause of upper limits to the evolution of CT_{max} is likely to be a biochemical trade-off: there are fundamental trade-offs at the molecular level between enzyme efficiency at normal temperature and enzyme stability at high temperature [51]. Variation in enzyme performance across temperatures also typically shows a gradual increase towards the optimum temperature and then a sharp decline near the upper thermal limit. Thus, optimal performance temperature and CT_{max} of most terrestrial species is already close to the hard upper limit of CT_{max} [52]. Key, and presumably costly, innovations and large-scale molecular evolution to a state that is significantly different from the phenotypes that currently exist within populations are required for species to function at or above this upper limit [53].

Although rapid adaptation can play an important role in the persistence of species under climate change (Figure 2), it is also clear that there are evolutionary and demographic limits. Populations may go extinct before adapting or they might fail to adapt (despite selection), because the traits under selection do not have sufficient variance in the direction imposed by selection. Such limits could determine which species persist and which do not. Such limits may also determine which traits adapt within a population [8]. For example, if the critical thermal maximum cannot evolve to deal with higher temperature, behavioural traits, such as microhabitat preferences, may come under selection instead [54]. Shifts in these behavioural traits will be likely to have follow-on effects on other traits affecting fitness [55,56].

Phenotypic Plasticity

While the breeder's equation is a useful heuristic for predicting evolutionary change across generations, it does not adequately describe phenotypic plasticity; the capacity for organisms to modify their traits within their lifetime in response to environmental conditions (Box 1). Nor does it capture the complex interplay between plasticity and adaptation [57]. There is substantial evidence that thermal physiological traits are plastic (Box 2); changing reversibly on time scales ranging from minutes (hardening) to days or months (acclimation) [37,58,59]. This plasticity can either retard or enhance the potential for rapid evolution under climate change (Figure 2). Behavioural plasticity — *e.g.*, active thermoregulation and microhabitat selection in animals — can reduce exposure to extreme conditions and so buffer a population while (often) reducing selection strength (Bogert effect). For example, populations of *Sceloporus* lizards that were able to behaviourally thermoregulate by moving to more suitable microhabitats in their environment had conserved thermal tolerances, while a population with reduced access to thermal retreats (thus presumably experiencing stronger selection), showed increased heat tolerance [60]. Conversely plasticity might promote evolutionary response by reducing mortality (Figure 2), buffering populations from variation in the direction of selection, and by maintaining population viability under rapid environmental change, allowing time for the population to respond to selection [61].

It has long been suggested that extreme conditions might expose previously hidden genetic variation which could itself contribute to rapid evolution [62–64]. A recent meta-analysis found that, while parental effects could be responsible for much of this release of genetic variation in laboratory experiments, there is potential for genetic assimilation of novel phenotypes when the change in phenotype generated by plasticity aligns with the major axis of genetic variation in the stressed population [65]. This suggests that plasticity, by providing additional variance, could increase the rate of adaptive evolution of thermal physiological traits under climate change (Figure 2C), though clearly much will depend on the details of the plastic response and how adaptive that response is as the organism encounters new environments [61].

Plasticity, in its various forms, is itself a trait, and is thus expected to evolve (Box 3). This idea is intuitive in the context of extreme events, which can occur with little warning and test an organism's limits. Individuals who can rapidly adjust their limits will be favoured over those with less flexibility. To the extent that such plasticity has a genetic basis, and remains adaptive, then, we would expect it to evolve in response to extreme events. Much of the work on thermal physiology over the last several decades has shown that thermal physiological traits are often highly plastic. Therefore, much of the selection imposed on thermal physiology during extreme events might be on the plasticity of those traits, rather than trait means *per se*. That said, and while the current theory on all this is logical, the few experimental studies on climate-relevant traits provide little support for direct selection on plasticity [61,66].

Most evidence for trait plasticity comes from laboratory studies in which organisms are held under a range of temperature or hydric regimes to generate reaction norms, and these studies increasingly incorporate environmental variability [67]. For example, studies of reaction norm shifts in *Drosophila* species as a function of growth temperature identified significant shifts in size and other morphological characters across a range of temperatures [68]. For logistical reasons, however, relatively few studies have examined plasticity in natural settings. The primary difficulty with field studies of plasticity is recapturing and phenotyping the same individual at different times. As a proxy for recapturing the same individuals, however, such studies can examine changes in population mean phenotypes across seasons within the organism's generation time. Although imperfect, monitoring trait variation at small temporal and wide spatial scales is valuable because it can reveal the surprising extent to which plasticity is at play *in situ* (Box 2).

Geographic Trait Variation and Local Adaptation

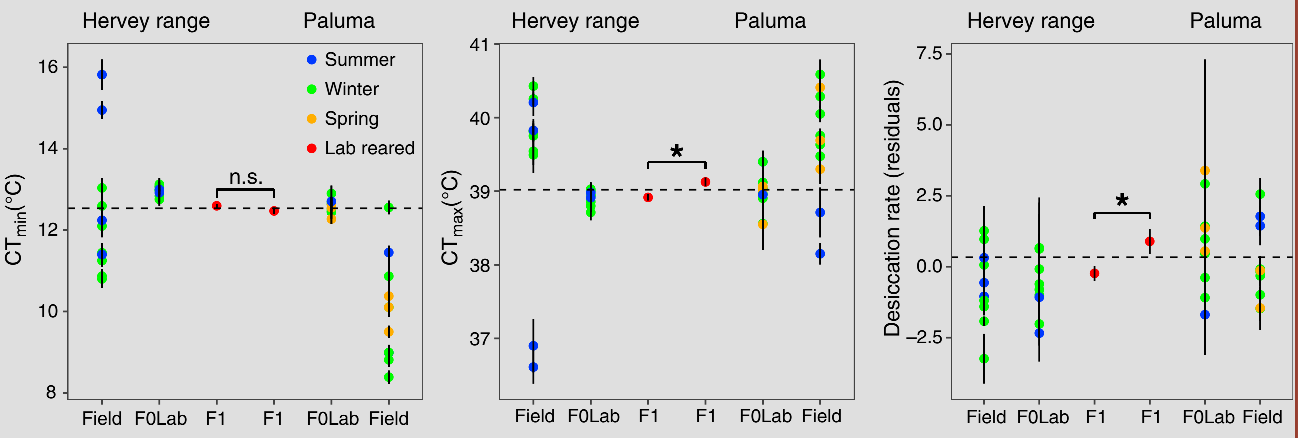
Evolved differences among populations within species, arising through local adaptation, provide a genetic resource that could be used by conservation managers to enhance evolutionary responses to rapid environmental change [69]. The concept of transferring 'pre-adapted' genotypes between populations to improve survival in future environments — targeted gene flow — is now well established among researchers [70], especially in relation to predictive and climate-adjusted provenancing of long-lived tree species in landscape restoration by selecting foundation tree seedlings across gradients in the direction of future climates) [71,72]. This strategy requires that the target phenotypes are not already present at sufficient frequency in the recipient population and that the focal trait has sufficient heritability for its frequency to increase with selection (Figure 2B). Of course, if populations vary in their genetically-determined capacity to mount a plastic response, transferring individuals to increase plasticity might also increase resilience (Figure 2C) [73,74]. The overarching question is whether among-population variation in climate-relevant traits, or in plasticity of these traits, is under substantive genetic control.

Studies of variation in climate-relevant (mostly thermal) traits across environmental gradients have provided extensive evidence for variation among populations in plants [27,75],

Box 2. Case study: Trait variation through space and time in a tropical lizard.

To illustrate how climate-related traits can vary within and across populations, and the various ways by which plasticity can contribute to this variation, we consider evidence from a tropical ectotherm: the southern rainforest sunskink (*Lampropholis similis*). This lizard species is predicted to be vulnerable to climate change because it has low dispersal and so will not be able to migrate fast enough to track its preferred climate and because it is a tropical rainforest-edge specialist assumed to be physiologically vulnerable to increased temperatures and lower rainfall [114,115]. Despite this perceived vulnerability, sunskink populations experience a wide range of thermal and hydric conditions across different elevations and latitude. In sunskinks collected in the field, climate-relevant traits (*e.g.*, critical thermal minimum (CT_{min}), critical thermal maximum (CT_{max}) and desiccation rate (DR)) show substantial and climate-correlated variation among populations, suggesting that these traits are somehow adjusted to local climate [116]. In a reference population towards the species' southern range limit, there is medium to low heritability for thermal physiological traits ($h^2 < 0.31$), and higher heritability for desiccation rate ($h^2 \sim 0.42$) [41]. There is little evidence for genetic correlations between physiological traits, or for maternal effects. While these results from a laboratory colony of the reference population point to a low to modest capacity for rapid evolution within populations, they do not tell us whether differences among populations are partly genetic or entirely plastic.

To address this question, Llewelyn *et al.* [82] scored physiological traits in field-caught, laboratory-acclimated and laboratory-bred lizards from two populations: one in a small, lowland rainforest isolate subject to more extreme maximum temperatures and stronger drying (Hervey Range), and the other from well within montane cloud forest (Paluma). Lizards were collected from the field sites and immediately phenotyped. These field measures were compared to the same traits following 6 months of acclimation to laboratory conditions, and in lab-reared offspring (see figure below). Lab-acclimated lizards exhibited a marked reduction in variation for the thermal traits CT_{min} and CT_{max}, indicating a strong acclimation response in these traits (but not in desiccation resistance). In lab-reared adults population differences in CT_{min} and CT_{max} were absent or small, whereas population differences in desiccation resistance were maintained. Egg incubation temperature (not shown) had negligible influence on adult thermal traits, but desiccation resistance was higher in adults raised from hot eggs, indicating developmental plasticity for desiccation resistance. These results show that most variation in thermal traits observed in the field is due to reversible plasticity and that lab-based measures massively underestimate variation in these traits. In contrast, desiccation resistance [116] shows developmental plasticity, higher heritability within populations and evidence for fixed genetic differences across populations.



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Trait plasticity and adaptive variation.

(Left) Critical thermal minimum (CT_{min}), (Middle) Critical thermal maximum (CT_{max}) and (Right) desiccation rate for southern rainforest sunskinks. Results from two populations are shown in a reflected order. Sunskinks were tested immediately after collection from the field (field), after 6 months, acclimation to the lab (F0lab), and in the lab-reared F1 generation (F1). Plot points represent mean ± SE of (1) groups of sunskinks collected at different times/seasons for the field-collected generation (field and F0lab) or (2) all the F1s from the same population. Colour indicates the season the parental generation was collected. The dashed horizontal line shows mean of the F1 population means.

Drosophila species [76,77], marine invertebrates [78–80] and reptiles [45,81,82], among others. Desiccation resistance has been found to vary spatially due to plasticity in plants [83] and reptiles (Box 2). That such variation is adaptive has occasionally been demonstrated by showing that populations perform at their peak under the conditions experienced in the region where the population originated. Experiments have identified among-population adaptive variation in traits such as heat-shock protein production in corals [78], growth potential in palms [84], lethal temperatures in snails [80] and thermal performance in anole lizards [45].

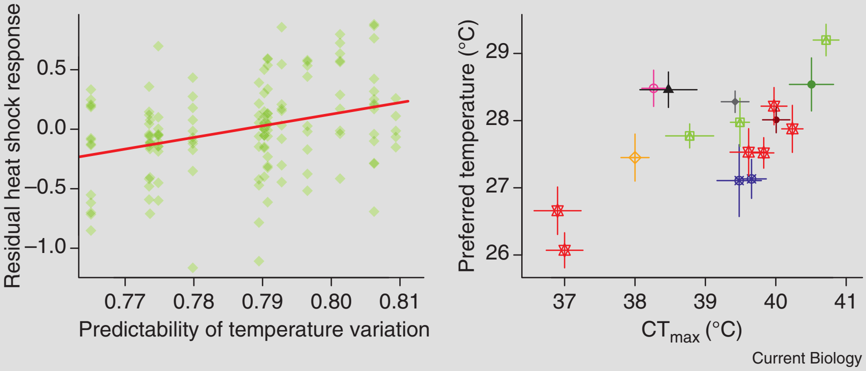
Whether such geographic variation has a genetic basis, and whether it represents adaptation, is, however, a challenging question to answer, except in model organisms. To meet this

Box 3. Case study: Predictability and complexity of plastic responses.

Plasticity is also a trait that can evolve, and thus might show local adaptation. The sunskink and its heat tolerance demonstrate this idea. Heat shock response (a rapid upward shift in CT_{max}) is smaller in sunskinks with higher initial CT_{max}, indicating a hard-upper limit to heat tolerance. In line with theory, however, heat shock response is larger in sunskinks from more predictably variable thermal environments [58]. These differences in heat shock response were still apparent in laboratory acclimated and bred lizads [58,82], suggesting fixed differences between populations.

Plastic responses do not always show a simple causal relationship with the environmental variables that drive them. They can also be affected by other physiological or behavioural traits. As well as responding to sudden heat exposure, CT_{max} in sunskinks acclimates in response to thermoregulatory behaviour. Sunskinks from cooler populations, and those tested in cooler seasons, prefer higher body temperatures, and because CT_{max} is plastic, this translates into a countergradient: lizards from cooler sites have higher CT_{max} than do those from hotter environments [117]. Comparisons among lizard species in this rainforest system also point to a dominant effect of thermoregulatory behaviour on variation in CT_{max}, whereas other thermal traits are more directly influenced by local environment [118].

These observations show that there is variation among populations in the degree of plasticity in some traits, such as heat shock response, and that this variation is correlated with the predictability of the environment, suggesting local adaptation of plasticity. It is also clear, however, that plastic responses can be complex, with plasticity in one trait (thermal preference) going on to affect the plastic expression of another trait (upper thermal limits).



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Complex causal relationships between climate variables and trait variation.

(Left) Sunskink heat shock response (controlling for initial CT_{max}) versus predictability of temperature variation at lizard collection site. Plot points indicate individual lizard responses. Lizards at the same position on the x axis are from the same population. (Right) Sunskinks collected from cooler sites, or in cooler seasons, select higher body temperatures and have higher CT_{max} than individuals from hotter sites and seasons. Plot points indicate collection group mean, and error bars show standard error. Points of the same colour and symbol are groups of sunskinks collected from the same site, at different times of the year.

challenge, several promising techniques have recently emerged to identify adaptive geographic variation *in situ*. The first technique exploits genomic data to identify genes with strong environmental associations [85], for example, single nucleotide polymorphisms (SNPs) with significant association to temperature and aridity were identified on all chromosomes of a *Eucalyptus* tree species [86]. To the extent that environment-associated SNPs are located in genes also known to influence relevant traits in model species, these could represent good targets for targeted gene flow [29,87] and for assessing whether adaptive alleles are already present at low frequency in prospective translocation sites [28]. The second promising technique requires phenotypes rather than genotypes and exploits measures of connectivity between populations to identify environment–trait associations that are likely due to local adaptation as opposed to plasticity [69]. This technique has been applied to geographic variation in lizards [69,88], but given information on landscape connectivity can readily be applied to many existing datasets exploring geographic variation in phenotype.

Common garden experiments, however, show that much of the variation in thermal traits among natural populations results from a plastic response to the local environment [22,27]. This was strongly evident in our case study on sunskinks (Box 3). Such plasticity may also be useful in the context of targeted gene flow. Reciprocal transplant experiments show that populations can differ in the extent of plasticity for climate-relevant traits (genotype-by-environment interactions) across a wide range of taxa including terrestrial plants [22,89–91], dinoflagellates [92], *D. melanogaster* [93], reptiles (Box 2) and fish [94].

Why there is such spatial variation in plasticity is still under investigation. The ‘variability hypothesis’ posits that plasticity will evolve to be higher in predictably variable environments because it enables short-term matching between phenotype and environment [95]. However, capacity for plastic responses should be minimized in unpredictable or homogeneous environments because plasticity and phenotype generation are likely to carry a cost [96]. Intuitive as it may seem, support for this hypothesis is mixed: studies on *Drosophila* species explicitly testing the variability hypothesis found no association between plasticity of traits and variability of relevant environmental variables [97–99], though often variability is confused with predictability, potentially muddying results [100]. The case study on sunskinks (Boxes 2 and 3) is one of the few to make a clear distinction between predictability and variability of the environment and shows a clear relationship between heat-shock response and the predictability of the thermal environment. However, studies on *D. melanogaster* [101], limpets [79] and copepods [102] have not been able to identify any spatial variation in plasticity despite adaptive trait variation along environmental gradients. Thus, whereas the various forms of plasticity may improve population viability under changing mean and variability of climate, there is, as yet, insufficient evidence to support targeted gene flow from populations in high variability to low (but increasing) variability environments.

Conclusions and Outlook

In the eight years since the seminal review by Hoffmann and Sgrò [13], there has been an explosion of experimental and field work aimed at understanding the nexus between climate, behaviour and physiology in non-model organisms. Much of this work, and the rise of conservation physiology as a distinct field [30,103], reflects legitimate concern about the impact of rapid climate change and the capacity of populations to adapt to that change. This empirical work has shown that climate-relevant traits are indeed under selection in nature, that they often show local adaptation, and — perhaps most clearly — that plasticity in these traits is ubiquitous, often pronounced and multifaceted.

This empirical work also shows that predicting the adaptive response to climate change will be challenging. For a given climatic shift, organisms can respond across many traits (behavioural, physiological, and others) and display substantial plasticity in the process (Box 1). Plasticity can either help or hinder the adaptive response and could itself evolve in response to selection. In the face of such complexity, one would hope to find some powerful fundamental theory that renders the complexity tractable, but this seems unlikely. Theory, instead, tells us to expect complexity.

While we can expect complexity, we can also identify several important questions that will benefit from further theoretical and empirical treatment. First, under what conditions might we see plasticity promote the adaptive response? Here, most attention has gone towards the idea that plasticity might reduce the strength of selection, but the reverse is also possible (Figure 2C), and the capacity for plasticity to buffer demographic impact — and thus to promote adaptation over extinction — has barely been explored (Box 1) [65]. Continued experimental research on model systems, including a focus on understanding the genomic and epigenomic underpinnings of plasticity, coupled with demographic models, will increase our understanding of how plasticity can accelerate or decelerate the rate of adaptive evolution.

A second important question is how we might exploit geographic variation in conservation efforts to promote adaptation through targeted gene flow [29,104]. Central to this question is the problem of identifying how strongly a species is adapting to different aspects of climate: for example, a species might show strong local adaptation to temperature but only moderate adaptation to precipitation. Identifying the strength of adaptation across climate variables, and thereby selecting optimal pairs of populations for targeted gene flow, is an issue that has been poorly explored so far. This problem is complicated by the fact that we might observe geographic trait variation correlated with climate, but we can expect much of this correlation to be driven by plastic responses rather than local adaptation (Box 1). Here, new techniques are already being developed that allow us to discriminate between local adaptation and plasticity using data collected *in situ*, without recourse to common garden experiments (e.g., [69]). These methods will require new data, or synthesis of old data, and will, in the coming years, reveal much about adaptation to climate. Once we identify important climate axes along which selection occurs for a species, such as temperature or precipitation, as discussed above, we will be in a position to identify source and recipient populations, and we can move on to the problem of optimising the timing and size of an introduction (e.g., [105]).

Finally, a third important question revolves around the relative roles of changes in physiological limits versus broader eco-evolutionary processes in the evolutionary response of organisms [106]. While not a focus of our review, eco-evolutionary processes, especially changing biotic interactions, are likely to have a substantial effect on species' responses and exposure to climate change. Incorporating these processes requires a more holistic theory that incorporates not only adaptation and plasticity of physiological traits [107], but eco-evolutionary feedbacks as well (*e.g.*, thermal game theory) [108]. Plasticity, in particular, can play a complex role in eco-evolutionary dynamics [107]: no consistent rules on plasticity in eco-evolutionary dynamics are known, and extensive research is needed.

Answers to the above questions will come from ongoing work on fundamental theory and experimental systems. But at the same time, human-driven acceleration of climate change, coupled with reductions in the size and connectivity of habitat, means that we don't have the luxury of waiting to resolve these questions before taking action to manage populations. Habitat fragmentation through human development causes the erosion of genetic diversity through inbreeding and genetic drift [109], reducing the capacity for populations to adapt. Fragmentation also reduces gene flow between populations, preventing the spread of genotypes that may improve adaptive capacity. In addition, reductions in the structural complexity of habitats through agriculture or urbanization can reduce microhabitat availability. Where microhabitat simplification occurs, populations are expected to experience more extreme climate conditions, as they are unable to effectively regulate their thermal environment through microhabitat selection [60]. Increased exposure, of course, increases the rate of adaptation necessary for population persistence.

This accelerating crisis, which combines increased selection on species due to climate change with a reduced capacity for adaptation due to human-mediated landscape changes, requires that we begin applying our understanding of the broad principles in the field especially to vulnerable ecosystems and species. This approach has inherent risks and requires conservationists, governments, and the public to accept the risk of failure in individual experiments in return for a more general hope of persistence and recovery. In particular, we cannot be precious about genetic intervention, perhaps even including gene-drive systems [110], when we have already imposed intense selection pressures that threaten species with extinction.

A number of methods for improving the capacity of species to adapt to climate change illustrate the promise of a ‘take action’ approach. Climate-adjusted provenancing is already being applied to habitat restoration and may provide populations with an opportunity to respond appropriately using both genetic and plastic adaptation strategies [71,86]. A framework for choosing when to use assisted evolution of corals in important reef systems [28,111], and models investigating optimal timing and size of an introduction (e.g., [105]), provide starting points for development of assisted evolution strategies in other taxa.

In situ experiments represent only a few of the options available for improving the resilience of species and ecosystems under climate change and illustrate the value of acting promptly to reduce further damage. We should start now to use our broad but imperfect knowledge of genetic adaptation and plasticity in improving species’ resilience to ensure the persistence of our environment and its ecosystem services into the future.

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