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ADVANCED REVIEW

When will a changing climate outpace adaptive evolution?

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Abstract

Decades of research have illuminated the underlying ingredients that determine the scope of evolutionary responses to climate change. The field of evolutionary biology therefore stands ready to take what it has learned about influences upon the rate of adaptive evolution—such as population demography, generation time, and standing genetic variation—and apply it to assess if and how populations can evolve fast enough to “keep pace” with climate change. Here, our review highlights what the field of evolutionary biology can contribute and what it still needs to learn to provide more mechanistic predictions of the winners and losers of climate change. We begin by developing broad predictions for contemporary evolution to climate change based on theory. We then discuss methods for assessing climate-driven contemporary evolution, including quantitative genetic studies, experimental evolution, and space-for-time substitutions. After providing this mechanism-focused overview of both the evidence for evolutionary responses to climate change and more specifically, evolving to keep pace with climate change, we next consider the factors that limit actual evolutionary responses. In this context, we consider the dual role of phenotypic plasticity in facilitating but also impeding evolutionary change. Finally, we detail how a deeper consideration of evolutionary constraints can improve forecasts of responses to climate change and therefore also inform conservation and management decisions.

This article is categorized under:
Climate, Ecology, and Conservation > Observed Ecological Changes
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KEYWORDS
adaptation, anthropogenic change, evolution, evolutionary constraints, forecasting

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1 | INTRODUCTION

Although scholars dating back to Darwin and Wallace believed that organismal evolution is a slow process proceeding over geological timescales, countless studies over the last few decades have documented evolution rapid enough to be observed over the human lifespan (Reznick et al., 2019). This genuine paradigm shift in our understanding of evolution has led many researchers to explore the scope of so-called "contemporary evolution." In particular, much effort has been directed toward understanding if contemporary evolution will be an important way that organisms respond to the multifarious threats posed by climate change (reviewed in De Meester et al., 2018; Hoffmann & Sgrò, 2011; Merilä & Hendry, 2014). Such studies unequivocally show that climate change can cause contemporary evolution. Nevertheless, it is far from certain that such evolutionary changes will be sufficient to allow populations to completely compensate for the effects of climate change (Radchuk et al., 2019).

In this review, we are necessarily approaching this problem through an adaptive evolutionary lens and the forces that shape, help, or hinder evolutionary responses to climate change. In the simplest sense, a few values will determine the rate of adaptive evolution: the intensity of natural selection imposed on a population, and the amount of heritable variation available to select from (Visser, 2008). In practice, however, additional variables influence this process (Alberto et al., 2013). For example, population size influences genetic variation, as more novel mutations are likely in large populations. By contrast, in very small populations, the outcome of evolution can be determined by genetic drift rather than selection (Gillespie, 2004). Likewise, connectivity between populations can introduce genetic variants from one population to another (Bontrager & Angert, 2019). Generation time, an emergent life history trait, can also affect the rate of evolution. All else being equal, shorter generation times will speed-up the evolutionary response to selection over time (Compagnoni et al., 2021). Whereas some factors, such as genetic correlations between traits or phenotypic plasticity, have the potential to either impede or promote evolutionary responses to selection (Futuyma, 2010; Ghalambor et al., 2007).

Distinct from asking how rapidly populations can respond to climate change is the question of how evolution leads to climate change adaptation? On one hand, evolutionary adaptations could allow populations to persist in-place. Adaptations that facilitate in-place persistence are likely to occur through the evolution of physiological traits such as heat and desiccation tolerance (Chown & Gaston, 2016). However, populations persisting in-place will also be challenged by changing ecological interactions, for example, via altered community composition or behavioral and physiological processes, imposing selection pressures across many other traits (Schleuning et al., 2020). On the other hand, evolution could lead to adaptations that facilitate climate tracking via shifts in geographic range and phenology (Parmesan, 2006). For example, the evolution of dispersal traits can facilitate geographic range shifts (e.g., Wellenreuther et al., 2022). Likewise, the evolution of responses to photoperiodic cues can facilitate tracking of changing seasons (e.g., Bradshaw & Holzapfel, 2006). However, just like evolutionary responses that facilitate in-place persistence, evolutionary responses that facilitate climate tracking might also expose populations to other novel selection pressures, such as via phenological mismatches with key interacting species (Cohen et al., 2018). As a common consideration for the evolution of traits that facilitate in-place persistence and climate tracking, trait variation can potentially be shielded from selection by plasticity that serves to slow or halt adaptive evolution to climate change. That is, plasticity can compensate for environmental change up to a point—for example, behavioral thermoregulation in-place, geographic range shifts, or phenological shifts that can all serve to shield organisms from climatic extremes—and it is only when limits on plasticity are exceeded that the trait variation is then exposed to selection.

While predicting or even disentangling the multifarious nature of evolutionary responses to climate change might seem daunting, recent advances are giving us the tools to identify the factors most important for adaptation to climate change. In this review, we will discuss the research approaches used to identify evolutionary responses to climate change, highlighting their relative strengths and weaknesses. We then review the evidence in support of adaptive evolutionary responses to climate change and evidence against such responses, focusing on the factors that can constrain evolution. Finally, we critically review our ability to assess the evolutionary potential of populations to respond to climate change and the currently available methods used to forecast future responses. As a unifying theme across these different topic areas, we structure our review around the concept of whether adaptive evolutionary responses will be sufficient to keep pace with climate change, now and into the future (Box 1).

BOX 1 Keeping pace with climate change: Roles for adaptive evolution and other compensatory responses

Our review is structured around adaptive evolutionary capacity to keep pace with climate change. However, it is important to recognize that keeping pace with climate change, as a broad concept, can involve other non-genetic compensatory responses. Plasticity in behavioral, morphological, or physiological traits can allow populations to compensate for climate change in place or through climate tracking over space and time, that is, geographic range shifts and phenological shifts (Parmesan, 2006). In this broader sense, keeping pace with climate change encompasses processes that facilitate the maintenance of population size over time.

Importantly, adaptive evolution to keep pace with climate change is the only mechanism through which populations can potentially continue to respond to sustained climatic changes in their environment (Figure 1). By contrast, the upper bounds on compensatory plastic responses of climate-relevant traits (Sgrò et al., 2016), including climate tracking via phenological shifts and geographic range shifts (e.g., Cohen et al., 2018; Lenoir et al., 2020) cannot, on their own, change across generations. Furthermore, plasticity can shield variation from selection until environments become too extreme for populations to evolve in response (Section 4.5). Understanding population capacities for rapid evolutionary responses is, therefore, all the more critical, as populations could be abruptly exposed to highly novel climatic conditions once their thresholds for compensation via plasticity are exceeded (Buckley et al., 2015).

In effect, growing evidence that evolution lags behind the pace of climate change (Section 3.1) must be tempered by the potential contributions of other compensatory responses to keeping pace. However, the ability of adaptive evolution to keep pace with climate change nonetheless provides a longer-range estimate of population viability as the climate continues to change. Such capacities are therefore highly relevant for forecasting approaches (Section 5). Indeed, it has become generally accepted that evolution can occur on timescales that are similar to climate change: for example, the Intergovernmental Panel on Climate Change (IPCC) and Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) list evolution as a mechanism important for determining organismal responses to climate change (IPBES, 2019; Pörtner et al., 2022). Yet, there is a potential concern here in that recognition of the important role of evolution in shaping responses to climate change will be conflated with the idea that organisms can simply adapt their way out of climate change. In reality, there is no such body of evidence to support this idea, but rather there is a pressing need to take a critical look at whether populations can keep pace with climate change via evolution. Hence, adaptive evolution and the ability to keep pace with climate change occupy the balance of our review.

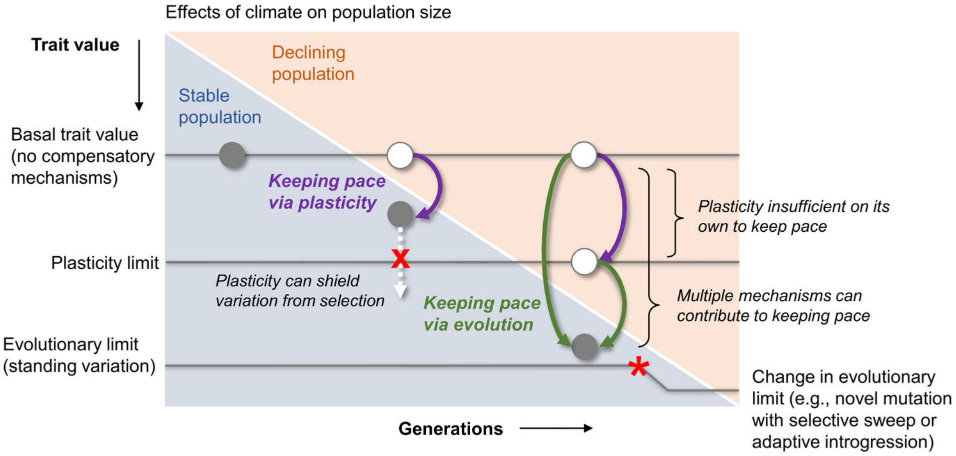

FIGURE 1 Mechanisms of keeping pace with climate change. Plasticity and evolution can contribute on their own or interactively to the ability of populations to keep pace with climate change. In some situations, plasticity and evolution can combine additively to facilitate population persistence. In other situations, plasticity can impede evolution by shielding variation from selection. Although multiple mechanisms can contribute to keeping pace with climate change, adaptive evolutionary capacity is a key determinant, as unlike plasticity, adaptive evolutionary capacity can increase across generations.

2 | ASSESSING (ADAPTIVE) EVOLUTIONARY RESPONSES

2.1 | Identifying evolutionary responses

There are a number of different approaches and lines of evidence that are used to study evolutionary responses to climate change, and each carries its own set of benefits and drawbacks. Because the nature of evolutionary responses is such that they span generations, much of the evidence for evolutionary change is retrospective or indirect. In this section, we consider different approaches to measuring or inferring past evolutionary change in response to climate change. In a later section (Section 5), we consider forecasting evolutionary changes to future climate change based on models and proxies of the potential for evolutionary responses of populations. Here, we provide a brief overview of approaches; for detailed reviews on this topic, see De Meester et al., 2018; Hoffmann & Sgrò, 2011; Merilä & Hendry, 2014.

Population monitoring and historical resampling provide information on trait or genotypic changes over time that can then be associated with climatic changes over the monitoring or sampling period (e.g., MacLean et al., 2019). While trait data are not sufficient on their own to demonstrate evolution, they provide patterns that might be consistent with evolutionary change. Genotypic approaches (e.g., molecular sequencing and QTL mapping), while useful for establishing genetic changes in populations over time, carry the limitation that they often do not have a direct connection with the phenotypic variation upon which selection acts. As a consequence, they are likely to overstate the contribution of loci of major effect and are typically unable to detect the hundreds or thousands of other loci that have small but nontrivial effects (Hansen et al., 2012). Further, for both genotypic and trait data, there is an added difficulty in being able to causally link organismal changes over time with climatic changes over the same period. In particular, it is difficult to rule out correlated evolution to other selective pressures that covary with the focal climatic selective pressures (e.g., Winn, 2004), or correlated evolution due to selection on other unmeasured traits (Mitchell-Olds & Shaw, 1987). Resurrection studies provide similar types of information, though because the historical samples can be revived, there is the possibility to assess genetic changes over time even with phenotypic traits as historical and modern populations can be reared under common garden conditions to assess the genetic basis for trait divergence (Geerts et al., 2015). Genotypic studies of resurrected and modern populations likewise provide inference into evolutionary change; though again, any resurrection study suffers from the issues of linking evolutionary change with climatic changes over the resurrection and modern time period. Resurrection studies also have the potential limitation of the "missing fraction" (Grafen, 1988), that is, there may be bias in the subsample of individuals that are capable of being revived, and thus, an inaccurate picture of evolutionary change over the given time period.

While space-for-time substitutions (Box 2) might not necessarily be biased by the missing fraction consideration, they can nonetheless be susceptible to site-selection biases. In addition, comparative analyses of populations experiencing different climatic regimes across spatial gradients, such as latitude or elevation, can be corroborated by common garden studies to demonstrate a genetic basis for trait changes (Kellermann et al., 2012). Contemporary space-for-time substitutions such as urbanization gradients operate in a similar manner, but might be able to isolate selection pressures with greater precision, assuming that study sites are selected carefully to isolate particular climatic drivers (Diamond & Martin, 2021b).

Experimental evolution studies provide an answer to the issue of establishing a causal link between climate and evolutionary change; however, the relevance of artificial selection in the laboratory and potentially strong biases of standing genetic variation in the starting population impose limits on the generalizability and biological realism of this approach (Harshman & Hoffmann, 2000). Quantitative genetics models including "animal models" provide an opportunity to closely track phenotypic trajectories, decompose the source of these changes into their evolved and plastic components, and to attribute changes to particular climatic variables, yet these approaches are data-hungry in that they require detailed information on relatedness, trait values and (co)variances, and fitness, measured over successive time points (Charmantier et al., 2014; e.g., Réale et al., 2003; Ozgul et al., 2009).

2.2 | Assessing the adaptive nature of changes

Although the methods described above are crucial for assessing whether evolutionary change has occurred in association with climatic changes in the environment, they do not provide information about the adaptive nature of those changes on their own. To assess whether the evolutionary changes are adaptive—that is, they confer a fitness benefit—

a number of phenotypic and molecular methods are available, though ideally both can be used to gain a complete picture of adaptive evolution to climate change. Reciprocal transplant experiments, in which populations (either contemporary or resurrected populations) are swapped between ancestral and novel environments (for climate change these could be historical and future-mimicking warmed environments), are frequently touted as the "gold standard" for demonstrating local adaptation (Johnson et al., 2022). Home-away and local-foreign advantages can each be tests of local adaptation, though the latter is often preferred to deal with the issue of fitness advantages even in overall mean low-fitness, degraded environments (Kawecki & Ebert, 2004). Home-away advantage describes the greater fitness of a given population in its home environment compared with the away environment; local-foreign advantage describes the greater fitness of the local population compared with the foreign population in a given environment. The main drawback of transplant approaches is that they are feasible for a limited group of organisms amenable to transplantation. There are also specific difficulties in using reciprocal transplant experiments in climate change research. If comparing adaptation in-place to contemporary warming, the historical unwarmed environment may no longer exist and can only be approximated, for example at higher latitudes or elevations (though, experimental manipulations added to reciprocal

BOX 2 Space-for-time substitutions over historical and contemporary timescales

The use of geographic variation in climate as a proxy for temporal changes in climate (space-for-time substitutions) can provide insight into the ability of populations to evolve in response to climate change (e.g., Stoks et al., 2014). For example, species that inhabit warmer climates at low elevations, low latitude, or shallow depths in aquatic habitats often have evolved higher heat tolerances than species that inhabit colder climates (Healy et al., 2019; Kellermann et al., 2012; Pereira et al., 2017), especially in marine organisms (Sunday et al., 2019). Similarly, species that inhabit dry environments often evolve greater desiccation tolerance (Kellermann et al., 2009), and some insects have evolved discontinuous gas exchange breathing patterns potentially as a mechanism to reduce respiratory water loss in dry environments (White et al., 2007). While these studies used common garden experiments to demonstrate evolution to local climatic conditions, others rely on comparisons of field-caught organisms across biogeographic clines that are consistent with climate adaptation, but not sufficient to disentangle the role of plasticity (Bennett et al., 2021).

The ability to evolve to keep pace with contemporary climate change has been inferred from such biogeographic and comparative studies in several ways. For example, a phylogenetic comparative study of historical rates of change in climatic niches suggests that rates of future climate change are likely to far exceed (by up to 10,000 times) rates of historical climatic niche evolution (Quintero & Wiens, 2013). Likewise, a comparative study in mammals estimated a several-million-year lag until biodiversity would return to current levels given historical speciation rates and contemporary extinction rates (Davis et al., 2018). Similarly, upper thermal limits are estimated to have only evolved at a rate of 0.784°C per million years in ectotherms, 0.593 in endotherms, and 1.3 in plants and algae (Bennett et al., 2021), but climates are expected to increase by ∼1.5 to 4.5°C (relative to pre-industrial temperature) in the next 100 years (Masson-Delmotte et al., 2021). While these studies suggest lags in evolving to keep pace with climate change will be the norm, it is important to bear in mind that average evolutionary rates are estimated over long geological scales, including periods of relative climate stability and likely slow rates of corresponding trait evolution. Thus, comparative phylogenetic approaches that estimate average rates of trait evolution over historical timescales are almost certainly at risk of underestimating whether species can keep pace with climate change via contemporary evolution.

As an alternative space-for-time substitution approach that ameliorates the issue of noncomparable timescales, urbanization gradients and their rapid spatiotemporal changes in climate are now being used as proxies of climate change (Tüzün & Stoks, 2018). For example, a comparative study revealed evidence of convergent evolution of heat tolerance to urban heat island effects across a range of different taxa and urbanization gradients (Diamond & Martin, 2021c). Interestingly, for a subset of species for which rates of trait change per magnitude of warming were available across biogeographic and urbanization gradients, there appeared to be little difference between historical and contemporary rates of change (Figure 2). Further, the magnitude of trait change was generally insufficient on its own to keep pace with the change in environmental temperature across the urbanization gradient. This suggests that evolutionary lags inferred from historical biogeographic studies might not be an artifact of timescale, as lags are also present in evolution to contemporary warming gradients.

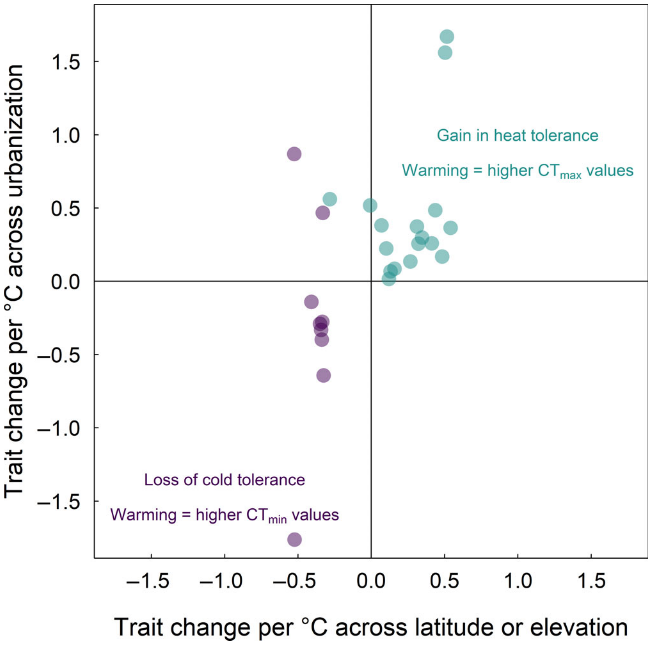

FIGURE 2 Magnitude and direction of the trait change in heat and cold tolerance per 1°C change in environmental temperature across urban heat island gradients versus across biogeographical gradients in latitude or elevation. Each point corresponds to one species' shift in thermal tolerance across urbanization and biogeographical gradients. Heat tolerance responses are represented by green symbols, and cold tolerance responses by purple symbols. Note that cold tolerance responses are presented such that the loss of ability to withstand cold temperature [or alternatively, higher critical thermal minimum (CT_{min}) values] is indicated by negative trait values. Reproduced from Diamond and Martin (2021c).

transplantation can get around this issue to some degree; e.g., Anderson & Wadgymar, 2020). For a broader range of populations, phenotypic selection measurements can provide evidence for adaptation by assessing changes in the strength and direction of selection over time in response to environmental change (Merilä & Hendry, 2014). Together with estimates of heritability, phenotypic selection can also be used to predict and evaluate post hoc, the evolutionary response to selection (e.g., Evans & Gustafsson, 2017; Grant & Grant, 2002). Molecular approaches can also be used to provide evidence of adaptation to climate, for example, through GWAS and related approaches that link genomic differences between populations to climatic variation. However, caution is warranted with these approaches owing to both known issues of statistical artifacts and biases, and the indirect connection between genotype-environment associations and actual responses to climate change (Hoban et al., 2016). Finally, developing a priori hypotheses regarding phenotypic and/or genotypic changes in populations and testing whether responses are of the expected magnitude and direction can provide yet another indirect line of evidence of adaptive evolution.

Sidebar: Role of plasticity in evolutionary responses to climate change

Although it is important to disentangle phenotypic plasticity—the expression of different phenotypes by a genotype in different environments—from evolutionary change, it is equally important to recognize that these mechanisms can influence one another. In particular, plasticity can act to facilitate or impede evolutionary change, and in turn, plasticity itself can evolve (Diamond & Martin, 2016; Ghalambor et al., 2007). In a changing environment, plasticity may impede evolution by shielding traits from selection, potentially leading to lagged evolutionary responses to further climate change (Buckley et al., 2015). A well-known representation of this is the "Bogert effect"—behavioral responses that enable organisms to track microhabitats and buffer performance loss in the face of environmental variation (Huey et al., 2003; Muñoz, 2022). However, plasticity rarely allows for perfect adaptation to changing environments (Diamond & Martin, 2021a; Ghalambor et al., 2007; Gunderson & Stillman, 2015), and so rather than halting evolution, imperfect plasticity may instead buffer populations in novel environments until evolutionary responses have sufficient time to occur (Diamond & Martin, 2021a). Alternatively, plasticity may shape the direction of evolutionary change in novel environments, leading to the evolution, or eventual loss, of plasticity itself (the "plasticity-first hypothesis"; Price et al., 2003; West-Eberhard, 2003). The role of plasticity in responses to climate change is an important area of current research (e.g., Charmantier et al., 2008; Donelson et al., 2018), and future studies should strive to holistically explore plastic and evolutionary mechanisms, along with their interactions (e.g., De Lisle et al., 2022; Swaegers et al., 2023).

3 | THE EVIDENCE FOR KEEPING PACE

3.1 | Adaptive evolution might not keep pace with climate change

Many studies have provided clear evidence of organisms having the capacity to adapt to climate change, including inferences from field experimental evolution and transplantation studies (e.g., Logan et al., 2014), field resurrection studies (e.g., Geerts et al., 2015), genotype–environment association studies (e.g., Vranken et al., 2021), and laboratory experimental evolution studies (e.g., Padfield et al., 2016). What is less clear is whether such evolutionary responses are sufficient to keep pace with climate change (Boxes 1 and 2). Combined meta-analytic and simulation modeling approaches indicate widespread evidence of lags in evolutionary rates of phenological change in birds (Radchuk et al., 2019). Strong explorations of whether evolution can keep pace with climate change (i.e., manipulative experiments) are more rare, but provide further evidence of lags. For example, Wilczek et al. (2014) transplanted banked seeds of *Arabadopsis* from different climatic regions into sites across the species' native climatic range and found that plants originating from climates that were historically warmer than the transplantation site consistently had higher fitness than plants native to that site, indicative of an evolutionary lag. However, this is not to say that lags are the only possible response. For example, a laboratory selection experiment in phytoplankton found evidence of rapid evolution of heat tolerance (via reduced metabolic rate and enhanced carbon-use efficiency) that was sufficient to maintain population growth rate under conditions that were 3°C above their initial thermal optimum for growth (Padfield et al., 2016; Figure 3). Similarly, a number of other experimental evolution studies show evidence of rapid evolution to climate (e.g., Mesas et al., 2021), and are at least suggestive of the capacity to keep pace with climate change.

3.2 | Metrics of evolutionary pace-keeping

Of course, pronouncements regarding whether or not specific populations will evolve to keep pace with climate change rely on assumptions that we are measuring the relevant quantities of interest. The prevailing view of widespread evolutionary lags with some exceptions of keeping pace or overshoot is reliant on the ability to measure changes in relevant climatic conditions as the organisms actually experience them (i.e., climate exposure) and on the ability to quantify rates of evolutionary change in key climate-responsive traits. Estimating climate exposure can present challenges, as quantifying microclimatic variation and the ability of organisms to exploit such variation while managing the costs and benefits of regulating climate exposure are not well-characterized for many organisms (Sinervo et al., 2010). Furthermore, there is equally the issue of choosing traits most directly responsible for keeping pace with climate change. For example, there is a relatively large number of studies demonstrating contemporary adaptive evolution of heat tolerance (Diamond & Martin, 2021c), but far fewer on other traits such as desiccation tolerance (van Heerwaarden & Sgrò, 2014), salinity tolerance (Coldsnow et al., 2017), acidification tolerance (Pespeni et al., 2013), tolerance of altered fire regimes (Keeley et al., 2011; Keith, 2022), and in sexually selected traits connected to aspects of organismal thermal biology (reviewed in Leith et al., 2022; for specific examples, see Calabrese & Pfennig, 2023; Moore et al., 2021).

Even fewer examine multiple climate-responsive traits within the same study system and context (Chown & Gaston, 2016). This is potentially problematic for two reasons. First, inferences regarding low vulnerability to climate change owing to evidence of evolution to keep pace in one trait could be misleading if another, unmeasured trait is equally important for survival and reproduction, but has a limited evolutionary response. A second, nonmutually exclusive issue is that there can be important interactions between traits, especially genetic correlations among traits that either tradeoff with one another or reinforce one another in response to climate change (Section 4.3), and which could alter perceptions of the ability of populations to keep pace (e.g., Garcia-Costoya et al., 2023).

While there is evidence of evolution of traits that directly compensate for the effects of climate change, there is also evidence of evolution of traits that mediate exposure to climate change. For example, evolution of cues to photoperiod

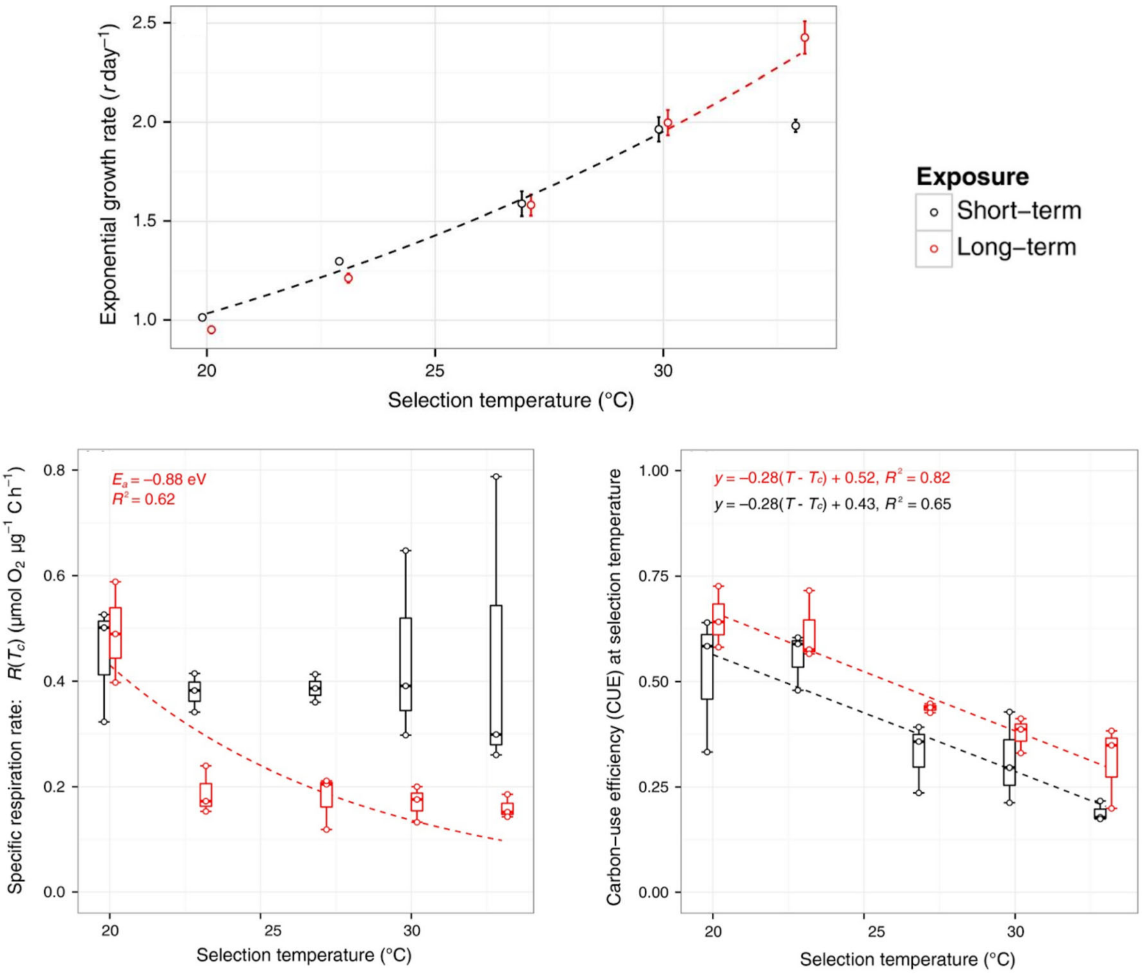

FIGURE 3 An example in phytoplankton of evolving to keep pace with climatic warming. Evolution of lower metabolic rate and higher carbon-use efficiency under experimentally warmed laboratory conditions contributed to overall higher heat tolerance and population growth rate. Short-term exposure to selection temperatures (10 generations) are represented in black symbols; long-term exposure to selection temperatures (100 generations) are represented in red symbols. The highest selection temperature of 33°C was 3°C beyond the starting population thermal optimum for growth. Modified from Padfield et al. (2016).

have evolved in pitcher plant mosquitoes in as few as 5 years to avoid unfavorable environmental temperatures (Bradshaw & Holzapfel, 2001, 2006). Further, reproductive phenology has evolved in arctic red squirrels in association with climate change, shifting the climatic conditions to which the squirrels are exposed toward those of their historical climatic niche (Berteaux et al., 2004). The evolution of dispersal at expanding range edges has likewise allowed species to track their historical climatic niches (Hargreaves & Eckert, 2014). However, it is important to be cognizant of the fact that phenological and range shifts need not invoke evolutionary responses, that is, keeping pace with climate change can occur through these mechanisms in the absence of genetic changes (Box 3). Though, plastic shifts in time and space might still mediate climate exposure and thus selection acting on climate-relevant traits (Kingsolver & Buckley, 2018). Finally, climate exposure can influence the relationship between the components determining the rate of adaptive evolution: for example, in great tits, positive covariance between the strength of selection and additive genetic variance in response to environmental heterogeneity had the effect of speeding up evolution to temperature rise (Husby et al., 2011; but see Ramakers et al., 2018).

3.3 | Variation among populations and species to keep pace

Under the assumption that the above-described methods yield reasonably accurate metrics of the capacity of populations to evolve to keep pace with climate change, it is obvious that there is substantial variation among

BOX 3 Distinctions between keeping pace with climate change versus rescue from climate change

The concept of keeping pace with climate change has parallels in the climate change "rescue" literature. Rescue from climate change describes the maintenance or recovery of population size as the environment changes. Like keeping pace, rescue involves genetic and nongenetic mechanisms (Figure 4).

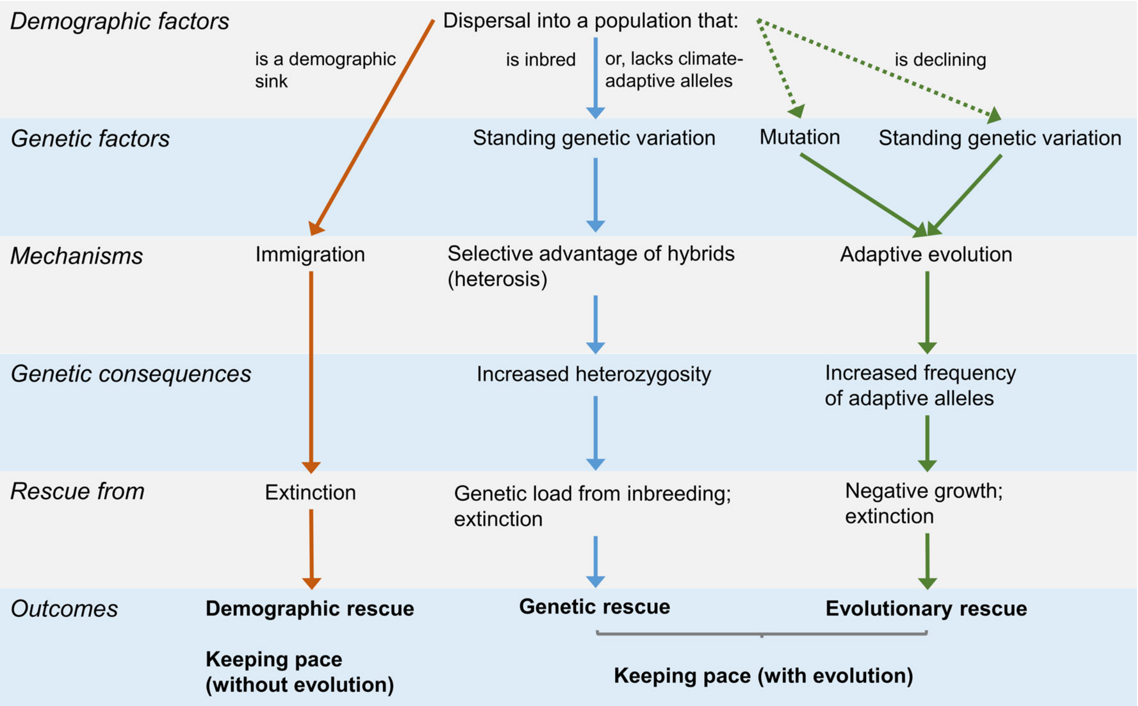

FIGURE 4 Different forms of rescue including demographic, genetic, and evolutionary rescue, in the context of genetic and nongenetic mechanisms of keeping pace with climate change. For dispersal into populations, solid lines indicate that dispersal is needed for that particular type of rescue, whereas dashed lines indicate that dispersal can accompany that type of rescue but is not a necessary condition for it to occur. Modified from Carlson et al. (2014).

Genetic rescue and evolutionary rescue each involve genetic changes in populations over time that allow for population persistence under environmental perturbations such as climate change. Genetic rescue describes the influx of new alleles into populations that are inbred and/or are lacking in climate-adaptive alleles despite having high genetic diversity. The influx of new alleles increases (climate-adaptive) genetic diversity and the likelihood of population persistence (Bell et al., 2019). Genetic rescue can be achieved via human-facilitated breeding of individuals with known genotypes and phenotypes and transplantation of these individuals into specific populations and locations (Hoffmann, Miller, & Weeks, 2021; Weeks et al., 2011), or naturally via immigration of new alleles into inbred populations (Bell et al., 2019). This type of rescue allows the population to keep pace with climate change without demographic loss. While there are many examples of human-facilitated genetic rescue (Hoffmann, Weeks, & Sgrò, 2021), we are also likely to observe natural examples of genetic rescue as species shift their geographic ranges in response to climate change. For example, warm-adapted populations might shift their ranges polewards in response to warming, and these warm-adapted populations might introduce new warm-adapted alleles into cool-adapted populations and facilitate survival with continued climate warming (Donelson et al., 2019). Evolutionary rescue, by contrast, specifically refers to genetic changes, either from standing genetic variation or new mutations, in a declining population that facilitates survival in a changing environment (Carlson et al., 2014). Although immigration is not a requirement for evolutionary rescue, there are cases where it can accompany this process, for example, by increasing standing genetic variation, generating more opportunities for new mutations to arise in larger populations, and mitigating Allee effects in populations structured by positive density-dependent growth (Bell & Gonzalez, 2011). Though, immigration could also harm evolutionary rescue if it occurs when there is already negative density-dependent population growth (Carlson et al., 2014). Under evolutionary rescue, while the population is initially in a state of not keeping pace with climate change and undergoing associated demographic losses, rescue of the population through adaptive evolution from standing variation and new mutations allows the population to enter a state of keeping pace and associated demographic recovery.

In contrast to both genetic and evolutionary forms of rescue, demographic rescue does not necessarily involve genetic changes in populations over time. In demographic rescue, the immigration of individuals into a sink population leads to increased population size which buffers populations against stochastic changes in population size and allele composition (Hufbauer et al., 2015). Thus, populations could keep pace with climate change via demographic rescue in the absence of adaptive genetic change. Although demographic rescue on its own does not require adaptive genetic change, the introduction of new individuals into a small inbred population is likely to both increase population size and genetic diversity, and therefore, many natural examples of immigration of new individuals into a population are likely to be examples of both demographic and genetic rescue. Indeed, demographic rescue is unlikely to be effective on its own over long periods of time, as climate change is likely to exceed the capacity of many organisms to cope with environmental change through mechanisms that do not rely on genetic changes, that is, via phenotypic plasticity (Huey et al., 2012).

populations and species in the ability to keep pace via evolution. Yet whether the magnitude of evolutionary lag is predictable based on population and species traits remains an open question. For instance, at the surface level, it would appear that an emerging theme is that organisms with fast generation times are those with the strongest evidence to keep pace, as shown in the laboratory experimental evolution study of phytoplankton thermal tolerance (Padfield et al., 2016). Nonetheless, there are exceptions, as shown in the field transplant study in *Arabidopsis* (characterized by a short generation time) demonstrating evolutionary lags in climate adaptation (Wilczek et al., 2014). Indeed, such methodological differences could be especially important to consider, as laboratory experimental evolution studies proffer a somewhat more optimistic view of the ability of *Drosophila* to keep pace with climate change (Harshman & Hoffmann, 2000) than field studies (Rezende et al., 2020; Santos et al., 2021). Further still, it is difficult to reconcile both of these *Drosophila* studies that provide evidence for some potential lags with field-derived evidence of rapid seasonal adaptation in this group (Rudman et al., 2022). As an added complication, generation time might be confounded with detection timeframes for assessing evolutionary pace keeping, as extirpation lags are likely to be longer in organisms with greater lifespans and time between generations (Figueiredo et al., 2019; but see Trisos et al., 2020 for a suggestion that abrupt extirpations might be expected for a broad range of organisms, with insufficient time for compensatory mechanisms to act).

More broadly, the physiological and ecological traits of species (and their shared evolutionary history) are expected to strongly affect extinction risk in the face of climate change (Huey et al., 2012). In conjunction, this trait variation can affect both the magnitude of selection imposed on the traits, and the ability of traits to buffer organisms from such selection. For example, population declines have been greater among bird communities compared to mammal communities in the Mojave desert over the past century of warming, perhaps due to microhabitat use among mammals (Riddell et al., 2021). Interestingly, species-level traits associated with evaporative cooling, such as body size and diet, explained population declines within these same bird communities, with larger species and those relying on animal diets for hydration experiencing the steepest declines in the desert environment (Riddell et al., 2019). Of course, populations will not only need to keep pace with the rate of environmental change, but also with the organisms with which they interact (Schleuning et al., 2020). Consequently, a population might track its abiotic niche but over- or under-shoot species they rely upon ecologically (Cahill et al., 2013; Parmesan, 2006). With the ever-growing body of literature that either directly addresses evolutionary adaptation to keep pace with climate change, or at least reports the quantities to allow computation of keeping pace metrics, there is a ripe opportunity to perform a quantitative synthesis of the magnitude of evolutionary lags including potentially critical modulators of the lag.

4 | CONSTRAINTS ON EVOLUTIONARY RESPONSES

Although some organisms are adapting to climate change, empirical evidence indicates that their responses are often slower than the rate of environmental change (Fréjaville et al., 2020; Radchuk et al., 2019; Wilczek et al., 2014). In some cases, such lags occur because climatic extremes cause natural selection to fluctuate too much for sufficient evolutionary changes to occur (Kingsolver & Buckley, 2015). However, analyses of many contemporary populations indicate that natural selection caused by climate change and other anthropogenic impacts is often adequate to promote rapid enough adaptation (Fugère & Hendry, 2018; Hendry et al., 2008). Therefore, it appears likely that other factors are preventing responses from keeping pace. Such limitations on the rate or direction of evolution in the face of natural selection are collectively known as "constraints" (Arnold, 1992; Futuyma, 2010); and they are known to affect those traits that facilitate adaptation to a warmer world (Araújo et al., 2013; Bennett et al., 2021; Hoffmann et al., 2013; Kellermann et al., 2009, 2012; Qu & Wiens, 2020).

4.1 | Limited genetic variation

Adaptation to climate change only occurs in populations that possess genetic variants that endow individuals with traits that are well-suited to warmer temperatures (Futuyma, 2010; Hoffmann & Sgrò, 2011). Thus far, it remains unclear whether or not populations possess the requisite genetic variability. On one hand, breeding and pedigree studies suggest that most populations harbor enough genetic variants to fuel adaptation (Bonnet et al., 2022; Moore et al., 2019). Targeted analyses have further revealed sufficient genetic variation to power evolution in key traits, like heat tolerance (Diamond & Martin, 2016). However, these studies' rosy outlooks might also overstate the genetic potential for adaptation. For instance, survival and reproduction are affected by temperatures that do not immediately cause lethal overheating (Huey & Kingsolver, 1989; Leith et al., 2022; van Heerwaarden & Sgrò, 2021), and genetic limitations in less-studied aspects of thermal performance could stymie adaptation to climate change (e.g., "thermal optimum" and "performance breadth"; Logan & Cox, 2020). Logan et al. (2020) detected that ladybird beetles lack genetic variation in all aspects of thermal performance other than the absolute limits, suggesting that performance at sub-lethal temperatures will still constrain adaptation to a sub-lethally warmer world. In severe cases, climatic fluctuations may be so extreme that the minimum genotype or phenotype necessary for survival and reproduction does not exist within the population at all, and the population immediately has no chance of persistence (see also Anderson et al., 2012). Many populations might also be flush with genetic resources as they begin adaptation, but then subsequently lose those genetic variants as natural selection purges them faster than new ones arise (Shaw & Etterson, 2012). Experimental evolution of copepods indeed showed that selection on upper thermal limits failed to produce adaptation as fast as rising temperatures because genetic variation became depleted (Kelly et al., 2011). Likewise, strong selection for higher heat tolerance in zebrafish potentiated a rapid initial pace of adaptation that eventually stalled due to the exhaustion of genetic variation (Morgan et al., 2020). Insufficient genetic variability is thus one factor that can grind adaptation to a halt.

4.2 | Too much or too little gene flow

Although a population's standing genetic variability determines if traits can adaptively evolve in response to climate change, migration can further add or subtract genetic variants. This gene flow among populations in divergent habitats is another oft-considered constraint (Hoffmann & Sgrò, 2011; Lenormand, 2002). In the context of climatic adaptation, gene flow impedes adaptation when individuals adapted to cooler environments bring their genes to warmer environments (e.g., Logan et al., 2016). The influx of cold-adapted genes can then prevent the population's average heat tolerance from tracking climate change across generations (Schiffers et al., 2013). However, recent genomic analyses have indicated that gene flow might not be as large of a constraint as once feared because even relatively weak selection against immigrants prevents poorly adapted alleles from establishing—particularly when there are locally adapted modifications to the whole genome (e.g., inversions, Tigano & Friesen, 2016). An alternative mechanism by which gene flow could influence adaptation to climate change is when immigration introduces beneficial alleles that arose in other populations (Kling & Ackerly, 2020; Kremer et al., 2012; Sexton et al., 2011). For instance, Bontrager and Angert (2019) simulated gene flow in wildflowers and found that populations exchanging migrants between similar warming conditions had fitter offspring than populations with no gene flow or than populations exchanging migrants between divergent warming conditions. Similarly, Razgour et al. (2019) showed that migration re-distributes beneficial alleles among bat populations and ultimately staves off local extinction. Collectively, these results indicate that gene flow is another force that determines a population's ability to keep pace with climate change.

4.3 | Misalignment between genetic covariation and direction of selection

Even when a population retains sufficient genetic variants for a trait to adaptively respond to climate change, the trait's evolution could also be restricted by natural selection on any traits with which it is associated due to pleiotropic or physically linked genes (Hughes & Leips, 2017; Shaw & Etterson, 2012). If the direction of natural selection is not aligned with the genetic covariance among all the genetically linked traits, adaptation to climate change is constrained because adaptive shifts for one trait generate nonadaptive shifts in the other(s) ("antagonistic selection"; Schluter, 1996; Walsh & Blows, 2009). This pattern could arise, for example, if two traits are positively genetically correlated and selection acts in opposite directions (e.g., size and age at maturity). Likewise, such misalignment can occur when two traits are negatively genetically correlated and selection acts in the same direction (e.g., offspring size and offspring number). It is important to note that genetic correlations are not a constraint on their own unless they are misaligned with selection (Agrawal & Stinchcombe, 2009). Indeed, Duputié et al. (2012) show that adaptation can be too slow or impossible without sufficient genetic correlations between important traits because the number of selective deaths required to mold each trait independently can be prohibitive. In many cases, these genetic correlations likely arose because selection favored individuals who possessed both traits in the historical environment (Arnold et al., 2008). Nonetheless, as our planet changes and the direction of selection along with it, misalignment between selection and the direction of genetic covariance may become common. Perhaps the most well-known example of misalignment between selection and the genetic covariance comes from a study of annual legumes. Etterson and Shaw (2001) transplanted northerly populations into southerly geographic regions that possessed the warmer and drier temperatures that were projected for the future. When the researchers then measured reproductive success and forecasted evolutionary responses for single traits in isolation, they found that there should be sufficient genetic variation to facilitate a rapid response to climate change. However, when the researchers incorporated the existing genetic correlations between several key traits into these forecasts, they found that misalignment between selection and the genetic correlations would cause traits to evolve >50% slower than if there were no genetic correlations at all. Experimental evolution in copepods further illuminates how misalignment between selection on physiologically correlated characters can preclude adaptation in a warmer world. For instance, elevated CO_2 both raises global temperatures and acidifies the oceans, yet antagonistic selection on physiological responses to warming and acidification prevents simultaneous adaptation to both threats (Dam et al., 2021; see also Kelly et al., 2016). Similarly, a two-decade study of wild ostriches revealed a genetic trade-off between cold-tolerance and heat-tolerance (Schou et al., 2022). As a result, the capacity for adaptation to more variable temperatures under climate change will be precluded because individuals who perform well under the increasingly frequent cold snaps will also perform much worse during the increasingly frequent heat waves, and vice versa. Thus, a single trait might have sufficient genetic variability for rapid evolution but fail to do so because of maladaptive responses in correlated traits.

4.4 | Demographic limitations

Beyond a population's genetic composition, a population's demographics can severely constrain adaptation to climate change. The foremost problem is that mortality—even predominantly of individuals with poorly suited phenotypes—shrinks population size and draws the population closer to an inescapable vortex of inbreeding, genetic drift, and extinction (Gilpin & Soulé, 1986). Gomulkiewicz and Houle (2009) showed that avoiding extinction at the hands of this "cost of natural selection" requires extremely large populations or higher-than-usual genetic variance for relevant traits (see also Haldane, 1957). In cottonwood trees, Blumstein et al. (2020) found that the mortality from natural selection in our warmer world is driving many southerly populations extinct despite considerable genetic variation in key traits. Mortality will also occur for reasons other than climate change—further reducing a population's size and also randomly removing genetic variants that could have aided adaptation (so-called "background selection"; Bell, 2013; Haldane, 1957). Finally, avoiding the "extinction vortex" depends primarily on the number of individuals who actually breed and pass on their genes ("effective population size"), which can be affected by many aspects of species' behavior or ecology (Holman & Kokko, 2013). Martínez-Ruiz and Knell (2017) examined how extinction risk was affected by reductions in effective population size due to mating skew—when most females mate with only a small proportion of the males. Here, intense mating skew slowed adaptation to a rapidly changing environment and promoted extinction in already small populations. Intrinsic species characteristics, like mating behaviors, can thus alter demography in a way that limits adaptive potential. Overall, these results indicate that demography alone can impede adaptation to climate change.

4.5 | Behavioral and phenological flexibility

A final constraint on adaptation to climate change is behavior and other forms of phenotypic plasticity. Animals often avoid stressful temperatures by moving into cooler microhabitats during the day's hottest hours (Buckley et al., 2015). Many plants and animals also ensure life-cycle events occur at the same temperature across space and time by undergoing those events earlier in warmer years (Badeck et al., 2004; Visser & Both, 2005). When organisms have control over their own temperatures in this way, individuals with poorly matched physiological tolerance can survive just as well as those with perfectly matched tolerance, and the population will not evolve much or at all (Huey et al., 2003). Indeed, a recent synthesis showed that physiological heat tolerance has evolved less between animal populations in behaviorally thermoregulating species than in nonthermoregulating species (Sasaki et al., 2022). Adaptation may similarly lag climate change because behavioral and phenological flexibility circumvents the need for evolution. Charmantier et al. (2008) also observed that phenological flexibility in breeding times from 1961 to 2007 allowed songbirds to match each year's spring temperatures, thereby obviating evolution during the timespan. However, although behavioral and phenological flexibility offer short-term solutions, rising air temperatures will eventually produce inescapably hot body temperatures (Buckley et al., 2015). Physiological tolerances will then be seriously mismatched from environmental temperatures, and the ensuing natural selection on physiological tolerance can cause severe mortality. For example, once environmental temperatures exceeded the capacity for Mexican lizards to behaviorally avoid the heat between 1975 and 2009, Sinervo et al. (2010) calculated that intense natural selection ultimately drove populations extinct before they could adapt. Behavioral and phenological shifts may thus constrain adaptation now and increase extinction risk later.

5 | PROMISE AND PITFALLS IN EVOLUTIONARY FORECASTING

5.1 | Evolutionary forecasting for biodiversity conservation

It is vital to understand the forces that have facilitated or constrained evolutionary responses to recent climate change, as it provides a critical baseline for our expectations of climate impacts on biodiversity. However, it is also important to be able to forecast future evolutionary responses to ongoing and future climate change (Urban et al., 2016). Forecasts of adaptive evolutionary responses to climate change rely on the same parameters as estimates of historical and contemporary adaptive evolutionary responses, that is, the magnitude and direction of selection and the amount of heritable variation upon which selection can act, but with the modification that these quantities are projected under future environmental conditions rather than examined contemporaneously or retrospectively. Forecasts likewise include modifiers of adaptive evolutionary responses such as plasticity, demographic feedbacks, and aspects of the genetic architecture (Section 1). Evolutionary forecasts can be used in several ways. For example, they can be used to refine predictions of ecosystem tipping points under climate change (Dakos et al., 2019); since there is currently appreciable uncertainty in the location of these tipping points, there is a need to better identify where these thresholds lie and to stay well below them. At a finer scale, evolutionary forecasts can help predict which populations will be more or less likely to keep pace with climate change in the future (Radchuk et al., 2019). This information can then be used to improve current conservation and management plans by targeting the most vulnerable populations for rapid, intensive interventions and supporting the persistence of less vulnerable populations (Prober et al., 2019).

In practice, there are a number of different frameworks that fall under the umbrella term of climate change vulnerability assessments or climate change risk assessments (Foden et al., 2019). Although these terms refer to systems in a broad sense, including interactions in the biodiversity-climate-society nexus (Pörtner et al., 2021), we focus on population-level responses of natural systems to match the scope of our review. Evolutionary responses to climate change impinge on each aspect of these risk assessment frameworks. For example, the IPCC AR6 climate risk assessment framework (Pörtner et al., 2022) encompasses four interacting components including vulnerability, exposure, hazard, and response (Figure 5). While the majority of the elements of our review can be considered as part of the vulnerability component (i.e., genetic variation and genetic architecture that determines the ability to adapt to climate change), evolutionary information is important for the other components as well. Specifically, in this context, "exposure" describes how strong climate acts as a selective agent; "hazard" describes the role of extreme climate events in shaping trait responses; and "response" describes the outcomes of iterative challenges imposed by climate change. For example, the winnowing of additive genetic variation under strong selection might limit population capacity to evolve

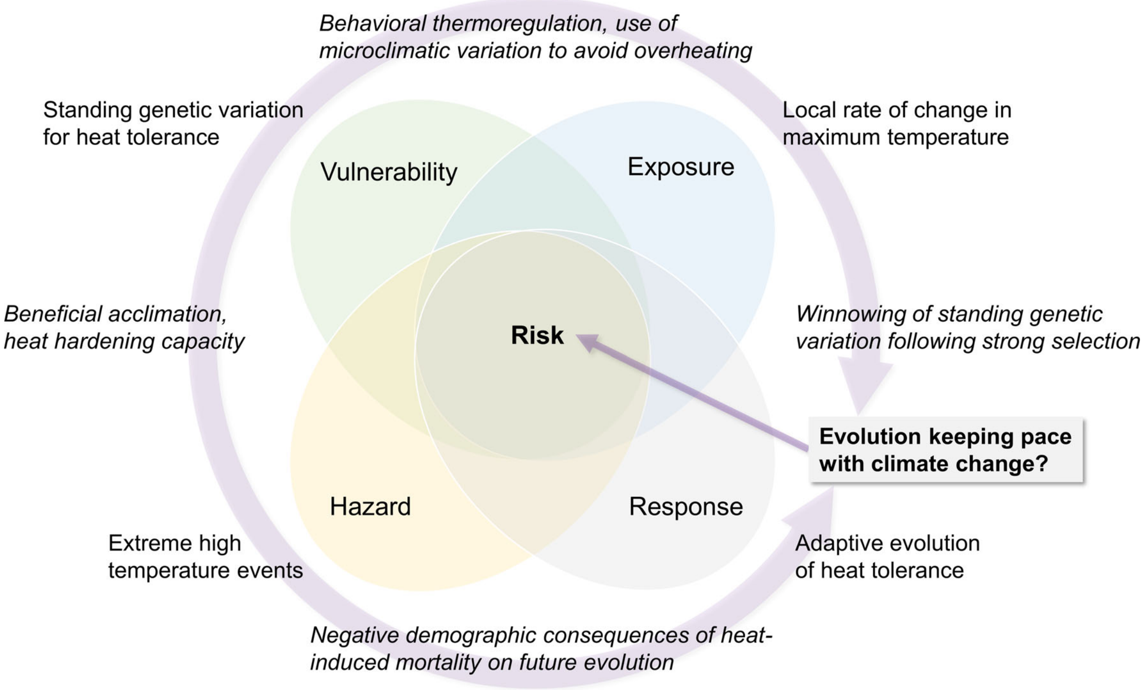

FIGURE 5 An illustration of the main factors and interactions of climate risk components (based on the IPCC AR6 climate risk assessment framework, which includes the components of vulnerability, exposure, hazard, and response). For simplicity, we focus on some key determinants of the evolution of heat tolerance in response to climate change. Though, this framework could be used to explore climate risk from an evolutionary perspective for a wide range of traits. The interactions among these climate risk components determine whether evolution will be sufficient to keep pace with climate change, better informing overall climate risk.

to future changes in the environment. In sum, the intrinsic capacity of populations to evolve to keep pace with climate change, and the extrinsic forces that facilitate or constrain these responses, are increasingly recognized as core components of climate vulnerability or risk.

5.2 | Evolutionary forecasting tools and uncertainty

When developing evolutionary forecasts to inform climate change vulnerability and risk assessments, it is important to recognize that there are different levels at which forecasts can be made. These span from population-level forecasts of particular climate-relevant trait values interpreted in context of projected changes in climate to forecasts of relative differences in vulnerability based on proxies of the potential for populations to evolve under climate change (Table 1). There are benefits and limitations to each approach, often representing tradeoffs between stringent data requirements that allow for quite specific predictions versus more broadly available proxies that allow for inferences across a range of species, but with much less precision. One early emerging theme is the potential for evolutionarily informed forecasts to yield qualitatively different results compared with evolutionarily naive forecasts. For example, evolutionarily informed species distribution modeling approaches that rely on current trait or genotype–environment associations and project population occurrences across space under future climates have revealed substantially lower vulnerability to climate (Figure 6).

Although it is impossible to determine whether these current evolutionary forecasts are accurate predictors of future population persistence, research from well-studied natural and laboratory systems suggests that, despite evidence of repeatable evolution to a shared climatic stressor (Diamond & Martin, 2021c; Donoghue et al., 2022; Moore et al., 2021; Ørsted et al., 2019), there can be substantial uncertainty in evolutionary trajectories. This uncertainty arises through two, nonmutually exclusive limitations on prediction: “random limits” and “data limits” sensu (Nosil et al., 2020). Random limits on prediction are driven by stochasticity in allele frequency changes under random genetic drift and by the random nature of mutations. By contrast, data limits on prediction are driven by an incomplete understanding and

TABLE 1 Summary of different evolutionary forecasting tools, including specific examples, and some of the benefits and limitations associated with each approach.

Forecasting approach	Examples and descriptions	Benefits versus limitations
Population-level forecasting of particular trait values or demography	Shefferson et al. (2017) forecasted evolution of the probability of sprouting in three species of orchid by using current vital rate–climate associations to model population demography under predicted future climates.	Projections include trait evolution and demography, but this approach requires considerable data input.
	Radchuk et al. (2019) compared actual evolutionary rates with critical rates for keeping pace with climate change across a broad range of species.	Projections cover a broad range of species, but this approach lacks demographic feedbacks.
Mechanistic species distribution models that incorporate evolution	Bush et al. (2016) used a standard quantitative genetics model to predict evolutionary responses in environmental tolerance traits of 17 fruit fly species to selection imposed by climate change in a spatially and temporally explicit context.	Projections differed substantially from those of distribution models lacking evolutionary information suggesting the importance of evolutionarily informed distribution models, but the approach requires a moderate level of data input.
	Razgour et al. (2019) developed genotype–environment associations for two bat species based on current climate and then compared projected distributions of hot-dry adapted bats and cold-wet adapted bats under climate change.	Projections show reduced species-level vulnerability to climate change when considering population-level variation in genotypes adapted to warmer, drier conditions, but it is unclear whether these conditions will be representative of future environments.
	Mechanistic species distribution models that allow for population variation in key parameters, for example, the magnitude and direction of selection and plasticity, and in turn, modulate the projected evolutionary response of performance and fitness (estimated via a quantitative genetics model) to climate change. For example, using this approach: the evolution of egg desiccation resistance alters expected mosquito distributions under climate change (Kearney et al., 2009), and the evolution of butterfly wing absorptivity is expected to initially allow montane butterflies to take advantage of climate warming, but later confers sensitivity to warming through evolutionary lags when the direction of selection shifts under climate change (Buckley & Kingsolver, 2019).	These models show a critical role for evolution in mediating species distributions under climate change, and highlight the importance of considering population-level variation in evolutionary parameters. Like many mechanistic approaches, these models are somewhat intensive with respect to the amount of data required to parameterize them. Though, such approaches could still be used more broadly than is currently appreciated.
Proxies of adaptive capacity	Genomic vulnerability to climate change relies on extant genotype–environment associations from different populations within a species range as an approximation of future persistence (Hoffmann, Weeks, & Sgrò, 2021).	Can be used for a broad range of organisms including long-lived species and species of conservation concern. The lack of causal association between genotype and environment can limit the reliability of this method (Hoban et al., 2016), though this can be ameliorated to some degree (Bay et al., 2017).
	Genetic diversity is a commonly used proxy of evolutionary potential, as more diverse populations are more likely to carry alleles	Increasingly available for a broad range of species, but there are issues with accounting for intraspecific variation (De Kort et al., 2021) and debate over the use of genome-wide

(Continues)

TABLE 1 (Continued)

Forecasting approach	Examples and descriptions	Benefits versus limitations
	that will be adaptive under ongoing climate change (e.g., Jump & Peñuelas, 2005).	genetic variation versus the subset of functional genetic variation that putatively affects fitness (Kardos et al., 2021).
	Population size is itself a proxy of genetic diversity, with greater population sizes expected to harbor greater genetic diversity (e.g., Hague & Routman, 2016).	Data on population size is already available for many species, but while there is generally a positive association between genetic diversity and population size, there are substantial differences in the scaling among taxa (Buffalo, 2021).
	Populations for which there is high additive genetic variance (estimated by variance-standardized heritability, and mean-standardized evolvability) in climate-adaptive traits are expected to persist under climate change (Thompson et al., 2023).	Estimates of additive genetic variance including heritability and evolvability provide direct information on adaptive capacity, and there is empirical support for an evolvability-adaptive divergence link (Opedal et al., 2023), but evolvability is often uncorrelated with heritability (Hansen et al., 2011, but see Hoffmann et al., 2016), and both are frequently measured under limited ranges of environmental conditions, and in the lab rather than more realistic field settings.
	For interspecific comparisons, high phylogenetic signal, or close resemblance between closely related species in climate-responsive traits can be suggestive of some shared genetic or developmental constraint that slows evolution (Bennett et al., 2021).	Phylogenetic signal is often readily available for many climate-responsive traits, but a high signal value is not necessarily indicative of evolutionary constraint (Revell et al., 2008).
	Organisms with faster generation times are expected to be better able to evolve to keep pace with climate change (e.g., Compagnoni et al., 2021).	Data on generation times are available for a moderate number of species (Sanderson et al., 2022), but this proxy of adaptive capacity is indirect, providing an upper bound on evolutionary rates, but no information on evolutionary capacity, that is, standing genetic variation.
Recent past contemporary evolution to climate as a proxy for future evolution to climate change	Rates and magnitudes of contemporary evolution to climate-relevant environmental variation (Diamond & Martin, 2021c; Sanderson et al., 2022) and inferences from experimental evolution studies under climate change-mimicking conditions (Kelly & Griffiths, 2021) can be used to calibrate expectations for future evolution to ongoing climate change.	Because these methods examine evolutionary responses, they might provide a better holistic understanding of population capacities to evolve in response to climate change; but, there is no guarantee that recent past climatic changes are representative of future climates.

measurement of evolutionary processes of a system, for example, unknown genetic correlations or epistatic interactions that affect evolutionary trajectories (Park et al., 2022) and/or by how data are used or modeled to forecast responses. Because the outcome of the effects of random limits and data limits on evolutionary prediction is the same (i.e., poor forecasting ability), and because random limits are essentially inherent in biological systems, the only way to directly assess whether predictions of evolutionary responses to climate change will be improved with additional data collection is to test the effects of data limits (both in terms of quality of the data and approaches used to model the data) on evolutionary forecasts in well-studied systems (e.g., Morrissey et al., 2012). However, since such opportunities are limited, it is prudent to continue to invest in the development and application of statistical tools to model typical scenarios encountered in natural systems that introduce apparent unpredictability into evolutionary forecasts. For example,

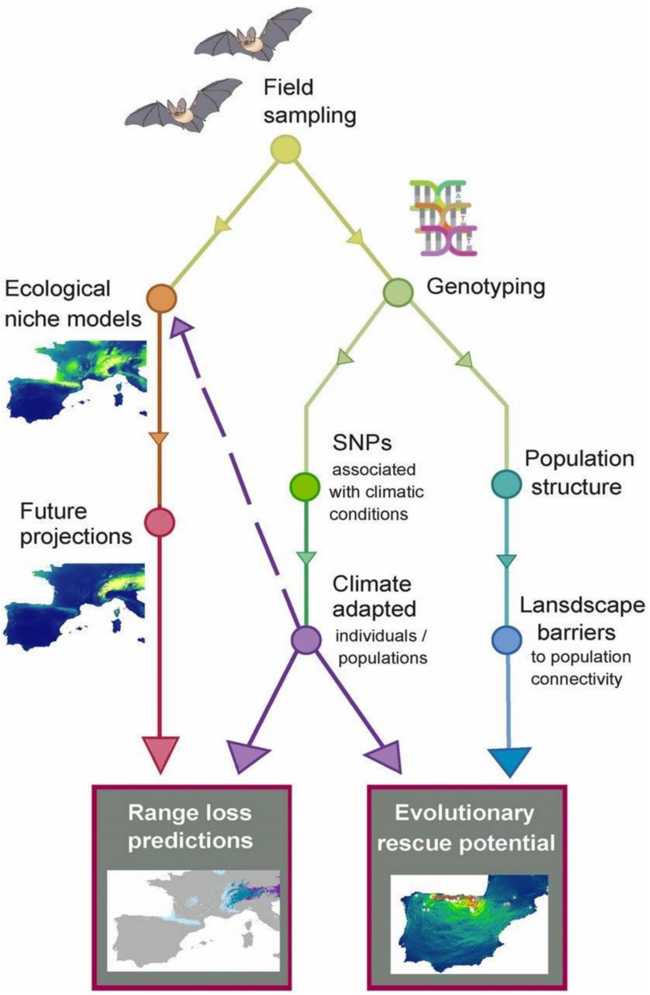

FIGURE 6 Integration of evolutionary potential estimated from genome–environment associations into species distribution models that forecast future range and distribution of two species of bats. Species-level vulnerability decreases when incorporating the potential for adaptive evolutionary changes in response to climate change. Reproduced from Razgour et al. (2019).

fluctuating selection (e.g., uncertainty in climatic variability), frequency-dependent selection (e.g., predator–prey dynamics), and sensitivity to initial conditions (e.g., rugged fitness landscapes with strong epistatic interactions), can be accounted for using Bayesian models of climatic uncertainty, autoregressive moving average models, and Bayesian sparse linear mixed models, among others (Nosil et al., 2020).

Although unmeasured or unmodeled factors can certainly play an important role in unpredictable evolutionary responses, there is equally the issue of the quality of the data already in hand. The components of forecasts based on quantitative genetics models and genotype–environment associations are sensitive to the environmental contexts in which they were measured. Few studies measure model components across a range of different conditions, least of all under simulated future conditions. For example, Santos et al. (2012) showed that methodological variation in how heat tolerance heritabilities were measured led to underestimation of additive genetic variance in natural populations. This study was motivated by the fact that there is support for rapid evolution of heat tolerance in *Drosophila melanogaster*, but that laboratory-estimated heritability in this trait was quite low. Indeed, heritability is notoriously difficult to estimate given its often potentially strong environmental contingency (Feiner et al., 2021). In effect, heritabilities are only directly meaningful for the context in which they are measured, and most studies estimate heritabilities under only the least realistic environmental conditions imaginable (i.e., the laboratory), nevermind the range of conditions that are ecologically important for the organism. Indeed, use of a common laboratory environment that was intended to reduce "noise" in the estimation of heritability of a trait across a range of different genotypes, could, as a worst-case scenario, cause each genotype under consideration to produce a totally different phenotype than it would in the wild, contingent upon the nature of the disparities between the laboratory and actual environmental conditions.

As a related complication, studies often do not estimate heritability in future warming contexts, so additive genetic variance might be misestimated for future responses. This is especially true given the potential for the release of cryptic genetic variation under novel environmental conditions (McGuigan & Sgrò, 2009; Noble et al., 2019). Yet, whether or not an environment is considered novel does not appear to have predictable effects on the structure of the genetic correlation matrix (Wood & Brodie, 2015) despite theoretical expectations that environmental novelty would disrupt typical correlations, specifically by weakening or even changing the directionality of tradeoffs between traits (Sgrò & Hoffmann, 2004). Together, these studies suggest that while the release of cryptic genetic variation is important to consider, it might be quite difficult to predict the nature of the outcome in novel environments.

Finally, even if the heritabilities of traits could be measured under conditions that replicate future climate change, there is still the issue of context dependency in how selection sees this variation. For example, the extent to which different populations are capable of using available microclimatic variation can be highly influential in determining climate exposure and thus the variation that is exposed to selection (Muñoz & Losos, 2018). Species with equivalent evolutionary potential to respond to climate change could have very different vulnerabilities if one is better at exploiting microclimatic variation to remain in more favorable climatic conditions.

Clearly, there are many sources of uncertainty in developing evolutionary forecasts, and many conceptual and modeling adjustments that can be made to improve the accuracy of forecasts. Yet it is worth taking a step back to reconcile the various calls for updates to forecasting tools with the scale of the problem at hand when it comes to incorporating evolutionary thinking into conservation plans. Thompson et al. (2023) summarized the outcome of a dialogue between evolutionary biologists and conservation practitioners with the joint goal of improving conservation plans. Echoing findings from previous work (e.g., Cook & Sgrò, 2019), Thompson et al. (2023) reiterated the important point that land managers and basic or fundamental researchers often call for different information on evolutionary potential, and that at the scale at which conservation practitioners are making decisions, often proxies such as population size, are used to form the basis of these decisions. This review also usefully provides a roadmap for when proxies or more detailed evolutionary forecasts are needed and will be most effective. A common suggestion across basic and applied researchers was for additional data on components and proxies of evolutionary potential. Indeed, even for well-studied species and species important for human health, there are strong limits on data availability for components of evolutionary forecasting models (Couper et al., 2021).

Uncertainty is not unique to evolutionary forecasting per se, but rather is a general issue of climate change forecasting. Yet, given uncertainty in evolutionary forecasting of population responses to climate change, it remains an open question as to exactly how evolutionary information could optimally be used in conservation planning and land management decisions. For example, "no-regrets" and "low-regrets" pathways, that is, interventions that carry low risk of unintended harm to ecosystems, often coalesce around bolstering habitat availability, quality, and connectivity. These interventions can relax selection pressures imposed by climate change on populations and can facilitate gene flow and geographic range shifts that can, in turn, affect the ability of populations to keep pace with climate change via evolution (Schloss et al., 2022). Climate-targeted measures tend to coalesce more around direct interventions to populations and are often associated with higher risk, that is, unintended, potentially harmful consequences of the intervention (Prober et al., 2013). For example, assisted evolution in corals involves laboratory artificial selection for greater heat tolerance of endosymbionts, which are then seeded in natural populations of corals in the wild in an effort to make them more resilient to bleaching (van Oppen et al., 2015). Similarly, hybridization of imperiled populations with less vulnerable populations, for example, through assisted colonization has been proposed to allow species persistence (e.g., Charles & Stehlik, 2021), with detailed guidelines to achieve the type of genetic amelioration required for particular populations (Weeks et al., 2011). More recently, genomic forecasting tools developed from plant and animal breeding populations in which breeding values are estimated from the sum of the additive genetic effects of all genome-wide markers have been proposed for application in developing climate-resilient natural populations (McGaugh et al., 2021). Yet, there is uncertainty both in terms of the inputs of identifying vulnerable populations for climate-targeted interventions and in the outcomes with unintended consequences of evolution-focused interventions such as disrupting critical species interactions (Ricciardi & Simberloff, 2009). On the one hand, many of these processes are already happening outside the bounds of human intervention, as species move to track their historical climatic niches and populations experience new opportunities for hybridization and other evolutionary responses, for example, to novel selective pressures (Larson et al., 2019). On the other hand, such targeted interventions can require substantial investment coupled with the risks of unintended consequences, thus raising the question of return-on-investment for these strategies (Filbee-Dexter & Smajdor, 2019). At the moment, enumeration of evolutionary considerations for climate change forecasts adds another dimension to the landscape of conservation and management decisions. The key major question to address in the near term is the scalability of evolutionary forecasting tools given the data-hungry nature of many of these approaches, and when proxies can and cannot be safely used.

6 | CONCLUSION

Although there is clearly more evidence of contemporary evolutionary responses to recent climate change than was previously thought possible, there is still often less change than is needed to keep pace with climate change (Radchuk et al., 2019). For this reason, the mechanisms that facilitate or constrain evolutionary responses to rapid environmental change are increasingly under investigation. These include considerations of standing genetic (co)variation, gene flow, plasticity, and demographic feedbacks (Hoffmann & Sgrò, 2011). An important takeaway from this body of research is that the same mechanism can facilitate or constrain evolutionary responses to climate change. For example, plasticity allows persistence under novel environmental conditions, but which ultimately shields variation from selection and limiting future evolutionary responses to ongoing climate change (Sgrò et al., 2016). Likewise, gene flow can act to bring in new alleles to populations that might confer advantages to cope with climate change (Brauer et al., 2023), yet high levels of gene flow could overwhelm locally adapted gene complexes within focal populations leading to population declines (Lenormand, 2002). Similarly, genetic covariation aligned in the direction of adaptive responses to climate change can facilitate population capacity to keep pace with climate change, yet genetic covariation with traits antagonistic to the direction of selection can limit evolutionary responses (Etterson & Shaw, 2001). An improved understanding of these factors that facilitate or constrain evolutionary responses to recent climate change might then be used to develop expectations, based on theory- and empirically-based rulesets, for which populations will be more or less likely to evolve to keep pace with climate change. Even so, there have been surprises in the form of mismatch between expectations and actual evolutionary responses and persistence under climatic warming for some well-studied populations. For example, the fast generation times and high amounts of standing genetic variation in many *Drosophila* sp. populations lead to the expectation that evolution will be able to keep pace with climate change (Harshman & Hoffmann, 2000). Yet this expectation is contrasted against field and laboratory experimental evolution studies showing limited evolutionary responses under warming (Santos et al., 2021).

The mismatch between expectation and actual responses to climate change would seem to arise from an incomplete knowledge of the system (e.g., unmeasured constraints) and from imperfect tools to detect, quantify, and predict evolutionary change (e.g., measuring heritabilities under conditions other than simulated future climate change, using proxies of fitness to measure selection rather than total fitness; Feiner et al., 2021; Morrissey et al., 2012). Mismatches might also be driven by the multifarious nature of climate change and the multifarious evolutionary responses populations undergo in response (Urban et al., 2016). While researchers can make informed guesses about which aspects of climate and trait responses are likely to be the most important, there will inherently be uncertainty in such predictions. In this context, it is worthwhile considering the ideal scenario for success in evolutionary forecasting, followed by what types of data are in hand and currently being collected, and finally what developing areas could prove useful in the future. Ideally, evolutionary forecasts would be developed with information on the initial amount and nature of genetic variation broadly and additive genetic variance in key climate-responsive traits, genetic covariation, generation time, gene flow, multifarious selection acting on the population, dispersal capability, phenotypic plasticity—especially in key climate-responsive traits, and information on current and future microclimatic niches. However, obtaining these data represents a substantial investment in time and resources (Nosil et al., 2020); the types of data more typically available at the present time are often incomplete compared with this list and/or rely on proxies of these factors (Thompson et al., 2023).

One way forward to overcome these challenges involves greater integration of genomic and phenotypic data. For example, the genome–environment associations that form the backbone of genomic vulnerability assessments could be validated, even for a subset of organisms, with field and laboratory experiments. Such an approach would determine cases where genomic tools can (and perhaps cannot) be used to make inferences about vulnerability to climate change (Hoffmann, Weeks, & Sgrò, 2021). Further, such genome–environment association studies could be united with contemporary space-for-time substitutions such as urban heat island gradients as a way of testing for rapid genomic signatures of change outside the current climatic range of the entire species. Genomic vulnerability estimates could then be linked with estimates of population persistence across the gradient to again validate the approach. Moving forward, it is important to continue to evaluate how evolutionary information in forecasts of responses to climate change alters these predictions and whether evolutionary trajectories are tracking or differ from those predictions as responses unfold in real time. It is likewise important to quantify the magnitude and nature of error in evolutionary forecasts when using incomplete data as this will help point researchers toward more useful proxies of evolutionary capacity to keep pace with climate change.

AUTHOR CONTRIBUTIONS

Ryan Martin: Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Carmen R. B. da Silva:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Michael P. Moore:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Sarah E. Diamond:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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IPBES Global Assessment Full report with chapter 4 (especially section 4.2.1.2) being the most relevant. https://doi.org/10.5281/zenodo.3831673

IPCC AR6 WG II Full report with chapters 2 (especially 2.4.2.8) and 3 (especially 3.3.4) being the most relevant. Retrieved from https://www.ipcc.ch/report/ar6/wg2/

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