

| OPINION

The Potential for Experimental Evolution to Uncover Trade-Offs Associated With Anthropogenic and Climate Change Adaptation

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ABSTRACT

Evolutionary responses to climate change may incur trade-offs due to energetic constraints and mechanistic limitations, which are both influenced by environmental context. Adaptation to one stressor may result in life history trade-offs, canalization of phenotypic plasticity, and the inability to tolerate other stressors, among other potential costs. While trade-offs incurred during adaptation are difficult to detect in natural populations, experimental evolution can provide important insights by measuring correlated responses to selection as populations adapt to changing environments. However, studies testing for trade-offs have generally lagged behind the growth in the use of experimental evolution in climate change studies. We argue that the important insights generated by the few studies that have tested for trade-offs make a strong case for including these types of measurements in future studies of climate adaptation. For example, there is emerging consensus from experimental evolution studies that tolerance and tolerance plasticity trade-offs are an often-observed outcome of adaptation to anthropogenic change. In recent years, these types of studies have been strengthened by the use of sequencing of experimental populations, which provides promising new avenues for understanding the molecular mechanisms underlying observed phenotypic trade-offs.

1 | Introduction

Evolutionary adaptation may provide a buffer against the full demographic impact of climate change, a phenomenon known as “*evolutionary rescue*” (Bell and Gonzalez 2009; Carlson, Cunningham, and Westley 2014; see Glossary). However, the factors (both biotic and abiotic) governing the potential for evolutionary rescue during climate change are not well understood (Nadeau and Urban 2019). Even less well understood are the potential side effects of climate adaptation; evolutionary changes in traits under selection very often lead to changes in other genetically correlated traits related to fitness, thus incurring

trade-offs (Etterson and Shaw 2001; Lande and Arnold 1983). These trade-offs and their underlying mechanisms are a crucial but understudied mediator of the response of populations to climate change.

Trade-offs occur when correlations among traits prevent the evolution of optimum values for all traits simultaneously (Agrawal, Conner, and Rasmann 2010). Some trade-offs occur because resources allocated to one trait reduce investment in other traits that require that resource (Houle 1991), and result in the compensation and redistribution of available energy to different processes under stressful conditions. At a genetic level, correlations

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can result when two or more traits are controlled by the same locus. In these cases, trade-offs occur through antagonistic pleiotropy, when selection opposes the direction of the trait correlation (Paaby and Rockman 2013; Saltz, Hessel, and Kelly 2017). An understanding of trade-offs is necessary to make accurate predictions of climate adaptation, which otherwise risk missing important constraints on adaptive change and thus overestimating a population's capacity to respond to future changes. Identifying the genomic architecture of adaptive responses may help to understand the amount of variation in key traits and to gain a mechanistic understanding of observed trade-offs.

Over the past two decades, an increasing number of studies have sought to test the potential for adaptation to climate change using *experimental evolution* (Figure 1), where populations of organisms are exposed to controlled sources of selection under laboratory conditions, and the evolutionary response is measured after a defined number of generations (Figures 2a and 3). This technique has a long history in evolutionary biology (e.g., Dallinger 1885), but has become increasingly popular over the past decades as an approach to predicting the effects of climate change (Figure 1a,1b). These studies have yielded important insights into future responses but may be limited by the constraints of laboratory systems, like smaller population sizes (and hence reduced genetic variation) and artificially stable environments (Hoffmann, Sgro, and van Heerwaarden 2023; Kawecki et al. 2012), which may lead to biased estimates of the total response. An important and underappreciated benefit of experimental evolution approaches, however, is the ability to measure trade-offs among traits and characterize the genomic architecture during climate adaptation (Figure 4).

Key principles regarding trade-offs have been characterized using experimental evolution studies (Figure 1). The idea that an organism can never reach optimal performance for all traits and that there must be a reduction in performance for one trait to improve another, is known as the Pareto front (Shoval et al. 2012). This idea applies to resource allocation trade-offs, such as trade-offs between fermentation and respiration (Li, Petrov, and Sherlock 2019), and life history traits, such as the trade-off between growth rates and life span (Biselli, Schink, and Gerland 2020). These key principles and insights into

trade-offs have been extensively utilized in agricultural research and enhancement, which aims to produce domesticated crops and livestock with high yields and disease or climate resilience. However, these two goals often oppose each other and are another example of the Pareto front (Shoval et al. 2012). For example, a key goal of many crop breeding programs is to improve drought tolerance, but improved drought tolerance often carries the trade-off of lower yield (Denison 2015; Lobell et al. 2014). Breeding programs focused on increasing the climate resilience of agricultural species (a form of applied experimental evolution) have provided important insights into trade-offs incurred during climate adaptation that can be applied to wild populations. For example, the trade-off between drought tolerance and yield has also been demonstrated in wild plants (Johnson, Hamann, and Franks 2022; Figure 3). The work described here from other fields have provided a broad foundation for understanding how trade-offs might limit adaptation to anthropogenic and climate change stressors. In this review, we highlight key principles of trade-offs during adaptation described in other fields and how they can be applied to better understand trade-offs during anthropogenic and climate change adaptation.

Studies testing for trade-offs in the context of climate adaptation have generally lagged behind the growth of experimental evolution as a tool for investigating climate change responses (Figure 1, but see Table S1). We argue that the important insights generated by such tests for trade-offs make a strong case for including these assessments when using experimental evolution to investigate responses to anthropogenic stressors and climate change in wild populations. Further exploration in laboratory studies would offer valuable insight into their impact on evolutionary trajectories and help create accurate predictions for expected outcomes in nature. Given that trade-offs are context-dependent and not easily predicted a priori, the observation of trade-offs depends heavily on experimental design. In Box 1, we provide a list of best practices for how to measure fitness to identify potential trade-offs during experimental evolution (see also Figure 2b). In Box 2, we highlight several caveats to consider when using genomic data to understand responses to experimental selection. In Box 3, we highlight an often-observed phenotypic trade-off between environmental *tolerance* and *plasticity* (Figure 3) and highlight a crucial methodological consideration.

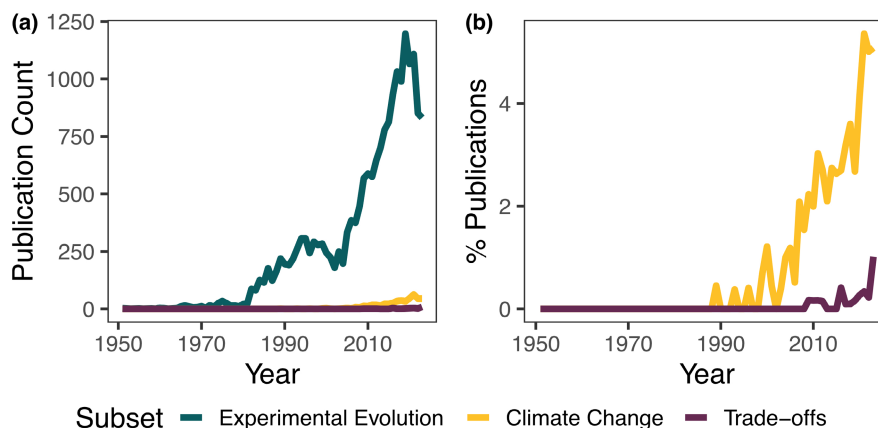


FIGURE 1 | Number of publications from 1950 through 2023 on experimental evolution, publications on experimental evolution and climate change, and publications on experimental evolution, climate change, and trade-offs (A), and the proportion of experimental evolution studies involving climate change and both climate change and trade-offs (B). The number of publications per year were collected from the Web of Science.

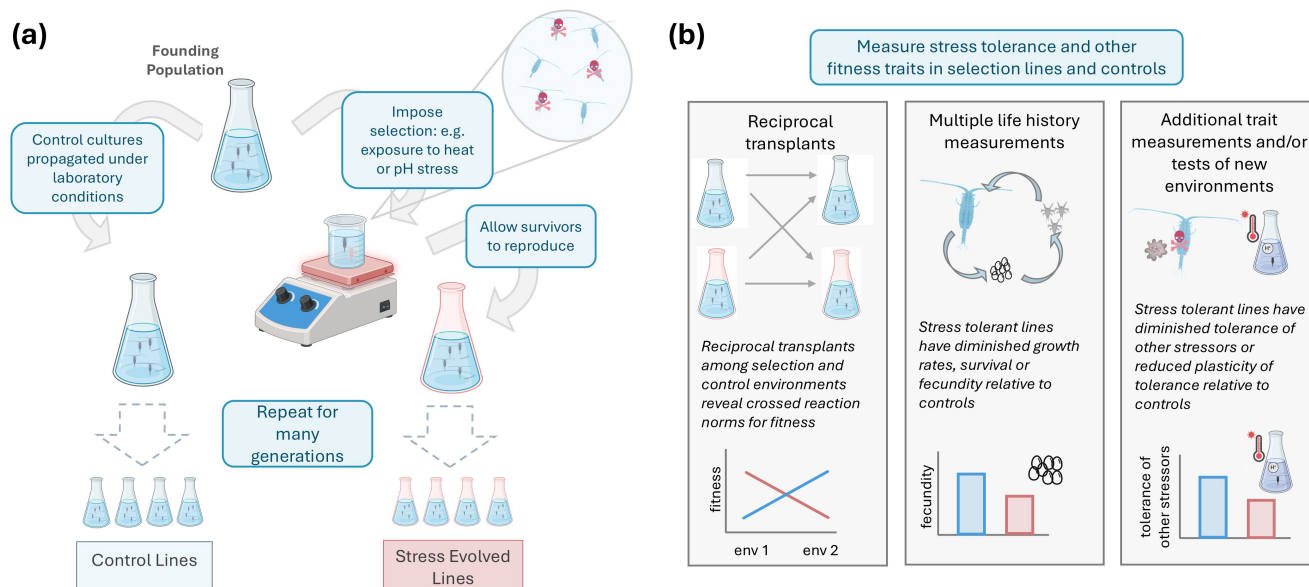


FIGURE 2 | (a) Conceptual schematic of experimental evolution design. (b) Various methods for measuring evidence of trade-offs that may have occurred during experimental evolution.

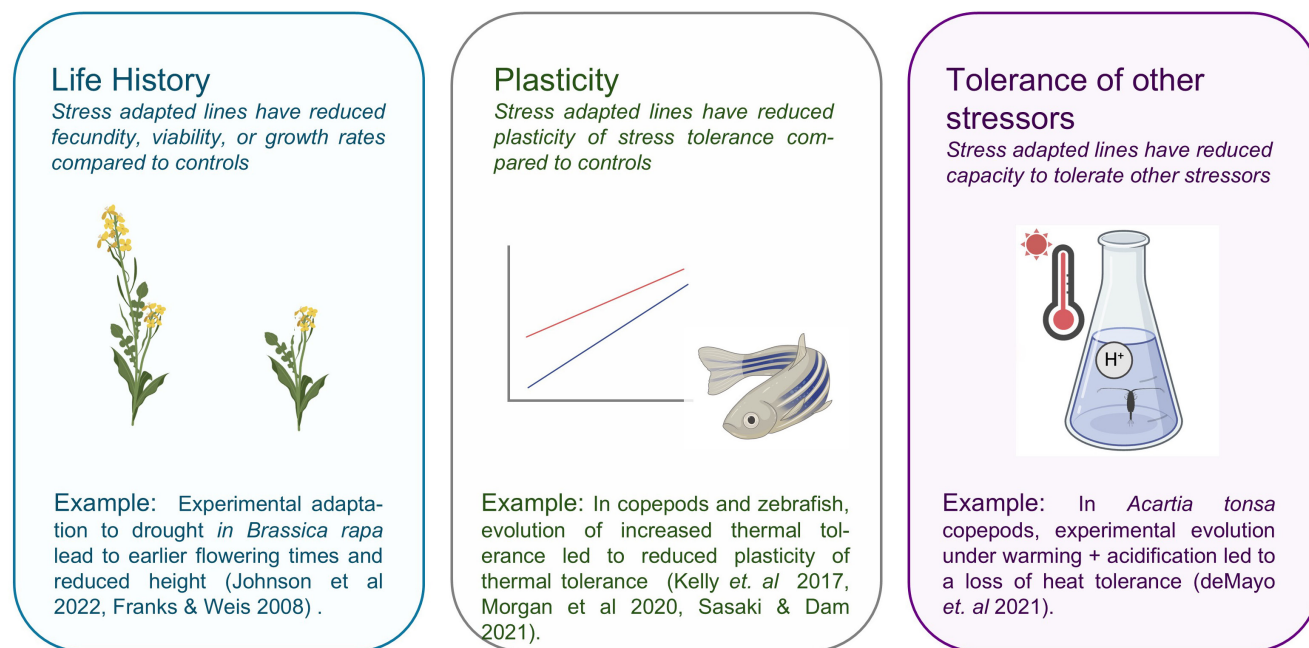


FIGURE 3 | Types of trade-offs observed during experimental adaptation to climate stressors with examples from the literature.

2 | Resource Allocation and Metabolic Trade-Offs

Organisms have finite resources that must be dedicated to a number of tasks to survive and reproduce. *Energetic trade-offs* typically take the form of fitness costs manifested directly through changes in life history traits such as growth, reproduction, or longevity (Figure 3). For example, reduced growth is commonly implicated in a metabolic trade-off with other energy-demanding processes such as acid–base balance (Garrett et al. 2020; Pan, Applebaum, and Manahan 2015). These resource allocation trade-offs often involve evolutionary conflicts

where differing selection pressures push a phenotype in opposing directions (Queller and Strassmann 2018). Functional trade-offs can also arise when two traits are mutually exclusive or biochemical pathways are shared by different responses forcing allocation to one versus another. For example, pH stress impacts the binding affinity of certain enzymes potentially altering osmoregulation and the ability to deal with oxidative stress (Silva et al. 2016; Stillman and Paganini 2015). One common trade-off occurs between parental survival and reproductive investment in offspring (parent–offspring conflict.) For example, there is often a decrease in offspring production associated

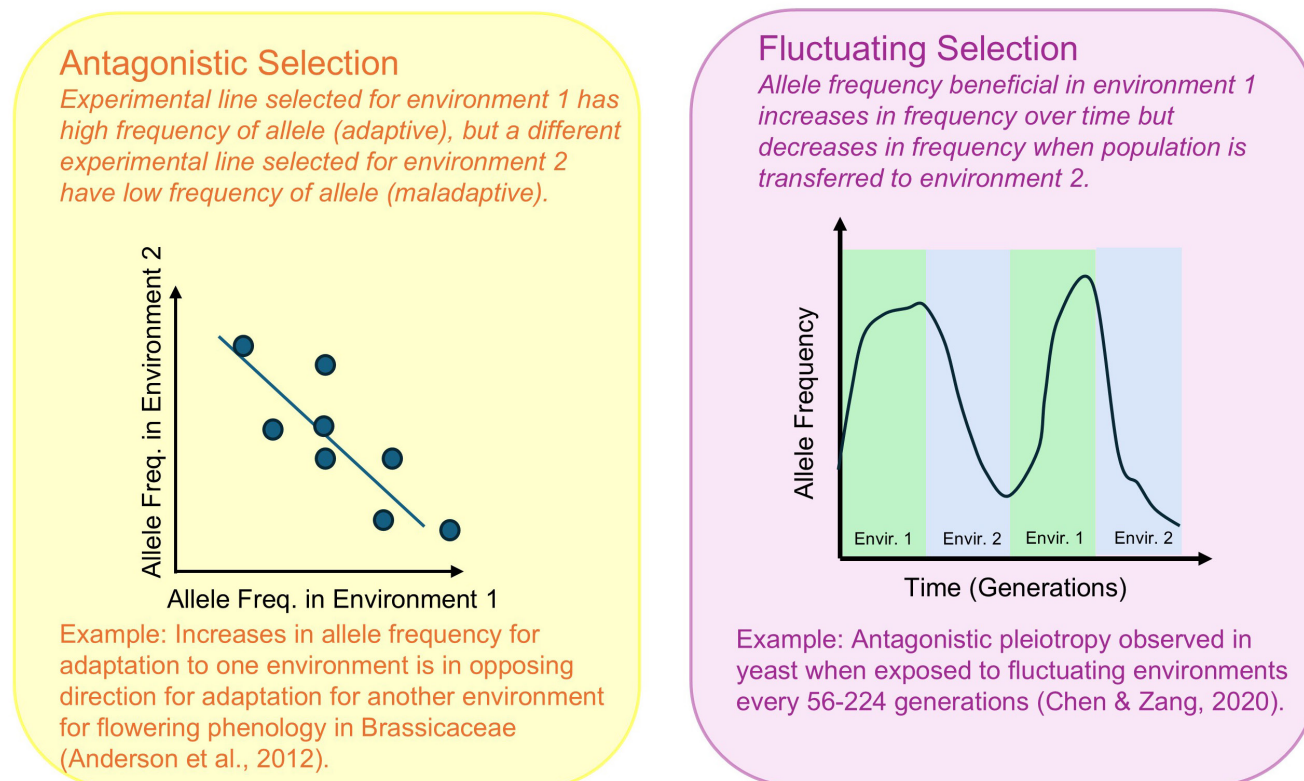


FIGURE 4 | Visualization of negative genetic correlations observed during experimental adaptation to climate stressors with examples from the literature.

with increased stress tolerance (Brennan, et al. 2022b; Kelly et al. 2016).

Conflicting demands between natural selection and sexual selection can also shape trade-offs, making evolutionary trajectories more complex and sex-dependent (male–female conflict) (Candolin and Heuschele 2008; Gissi et al. 2023). For example, male Trinidadian guppies with brighter tail colors attract more females but also are more easily detected by predators (Heinen-Kay et al. 2015; Magurran 2001). In this scenario, there is a trade-off between more noticeable tail color and morphology (driven by sexual selection) and survival (driven by natural selection through predation). Importantly, trade-offs are highly context-specific—In this case, selection pressures are dependent on predator visual capacity. Where human disturbance increases turbidity (reducing visibility and likelihood of detection by predators) evolution of male coloration and female preference is less constrained by this trade-off (Ehlman, Martinez, and Sih 2018; Ehlman, Torresdal, and Fraser 2020). This example illustrates how changes in the environment can shift the alignment (or misalignment) of different selective pressures, either reinforcing or dampening the manifestation of trade-offs in evolutionary dynamics. Similar trade-offs may occur across sexes if selection pressures act differently on males and females (Plesnar-Bielak and Łukasiewicz 2021). In *Drosophila melanogaster*, for example, there appears to be conflicting phenotypic optima for development time and fecundity in males compared to females in response to desiccation stress (Kwan et al. 2008). As a result, there may be reduced adaptive potential and average fitness of the population.

3 | Genomic Architecture of Trade-Offs: Linkage and Pleiotropy

Genetic correlations are the result of two traits controlled by a single locus (pleiotropy) or two traits that are controlled by two different loci, but are in linkage disequilibrium (LD) and are inherited together (Saltz, Hessel, and Kelly 2017; Sgrò and Hoffmann 2004). *Genetic trade-offs* occur if the two traits are negatively correlated with respect to the direction in which selection is acting on them—for example, if selection favors both more eggs and larger eggs but egg size and number are negatively correlated (Figure 4). In the case of experimental evolution studies, observed genetic trade-offs may be a result of strong selective pressures over a few generations, resulting in large linkage blocks under selection (Barghi and Schlötterer 2019). Therefore, a key difference between trade-offs incurred by pleiotropy and LD, is that recombination could eventually uncouple traits that are physically linked (although this depends on the duration and magnitude of selection). While it is extremely difficult to disentangle the causal mechanism of genetic trade-offs (pleiotropy vs. linkage), controlled laboratory conditions offer a unique opportunity to identify the loci responding to selection and loci involved in genetic trade-offs by tracking allele frequency changes over time during adaptation to experimental conditions (Figure 4) (Brennan et al. 2019; Griffiths, Kawji, and Kelly 2021; Kang et al. 2016; Martins et al. 2014). Chen and Zhang (2020) were able to demonstrate that the fitness trade-offs they observed in yeast were due to antagonistic pleiotropy. When yeast were exposed to fluctuating environments every 56–224 generations,

BOX 1 | Designing experiments to capture trade-offs and accurately predict evolutionary trajectories.

Trade-offs can only be identified by measuring more than one trait during experimental evolution (Figure 2b), but it can be difficult to predict *a priori* the most relevant or important traits to investigate. Furthermore, in an evolutionary context, it is particularly useful to examine how these trade-offs affect fitness. Different operational definitions of fitness, however, may yield different estimates of the impact of these trade-offs (McGraw and Caswell 1996).

Ultimately, the traits examined and fitness metric used need to balance logistical constraints, organismal life history, and the temporal scale of selection. Given the generally short timescales of interest in both experimental evolution studies and climate change, however, a relatively simple fitness estimate integrating survival and reproductive output (such as proposed by McGraw and Caswell 1996) may provide useful insights into the role trade-offs will play in shaping rapid adaptation. For example, without incorporating egg production rate, hatching success, and developmental survival into a fitness estimate, important trade-offs would have been missed in copepods subjected to ocean acidification and warming (Dam et al. 2021). It is important to consider several aspects of experimental design to maximize the chances of accurately detecting trade-offs incurred by climate adaptation (Figure 2a,b).

Experimental design considerations:

- Consider including multiple stressors, fluctuating selection, and/or increasing the number of generations exposed. Under these conditions, trade-offs can lead to important changes in the response to selection (Bono et al. 2017) that cannot be predicted *a priori* from single-stressor exposures. Of particular importance is understanding when trade-offs may dampen the effects of selection in multiple-stressor contexts (Orr et al. 2022).
- Consider adding a reciprocal transplant experiment (Figure 2b) following selection events to examine fitness consequences across environments, including fitness effects incurred by loss of plasticity (Demayo et al. 2021; Langer et al. 2019; Thor and Dupont 2015).
- Consider the strength of selection imposed and the effective population size. Stronger selection and smaller effective population sizes are more likely to lead to trade-offs and fixation of alleles with high levels of antagonistic pleiotropy (Otto 2004; Santos et al. 2023).
- Consider the source population used to found experimental populations, as genetic correlations among traits (and hence observed trade-offs) and the effects on fitness may differ among populations of the same species (Hoffmann, Sgro, and van Heerwaarden 2023; Kelly, Grosberg, and Sanford 2013).
- Consider other unmeasured traits which may interfere with the ability to detect trade-offs. For example, in the case of resource allocation trade-offs, variation among individuals in the ability to acquire resources may lead to positive correlations among traits that require that resource, despite an underlying negative resource allocation trade-off between those traits (Houle 1991).

BOX 2 | Genetic detection of trade-offs incurred during experimental evolution will depend on aspects of the experimental design.

The rate of recombination of the species and the polygenic nature of the trait, and epistatic interactions among loci contributing to adaptation all impose limitations on our ability to describe the genomic architecture of adaptation and trade-offs. However, they can be ameliorated by changes in experimental design. Additionally, laboratory settings are themselves a multistressor environment (e.g., high density environments, laboratory food, and treatment exposure) and adaptation to both laboratory conditions and treatment exposure could result in genetic constraints (pleiotropic effects) (Burny et al. 2022). To increase the statistical power for characterizing the genomic architecture of trade-offs and to account for laboratory adaptation, we recommend the following best practices:

- Reduce linkage disequilibrium:
 - Reduce linkage disequilibrium (LD) by increasing the number of generations allowing more time for recombination to break up large linkage blocks or by reducing the strength of selection. This will help genetically uncouple trade-offs induced by large amounts of LD and improve efforts to identify the causal loci.
 - LD can also be reduced by performing factorial crosses at the start of the experiment, which generates more haplotypes during meiotic recombination. This is especially important when using inbred lines where large blocks of loci in LD have been generated for the purpose of a reference panel. However, outbreeding the inbred lines can break up patterns of linkage before experimental evolution and then the known founder haplotype structure of the founding lines can be leveraged to better map causal loci (Brennan et al. 2019; Hsu et al. 2021).
- Control for laboratory adaptation during selection experiments:
 - *Ambient vs. Stressful Comparisons*: Laboratory adaptation can be partially accounted for by measuring changes that occur in replicates of both ambient and stressful laboratory exposure for the same number of generations.
 - *Stressful and Opposite Comparisons*: Organisms could be exposed to the same variable, but in opposite directions. For example, *Drosophila* that were exposed to both hot and cold treatments for more than 80 generations had gene expression changes in the same direction compared to a revived ancestral population that was attributed to laboratory adaptation, while gene expression changes in opposite directions to warm or cold fluctuating selection was attributed to temperature adaptation (Hsu et al. 2021).
 - *Ambient vs. Stressful vs. Ancestral comparisons*: Allele frequency changes during selection can also be partitioned into the total variance due to laboratory adaptation, selection, and drift using a covariance method comparing both ancestral and ambient populations to

(Continues)

BOX 2 (Continued)

selected populations, greatly increasing the accuracy of analyses attempting to identify true targets of selection (Brennan, et al. 2022a; Buffalo and Coop 2019, 2020)

- *Leverage advances in statistical methodology:* New methods have been developed that simulate the amount of expected genetic drift that occurs during selection experiments to establish thresholds for statistical tests used to identify loci under selection across multiple replicates (Kelly and Hughes 2019). These simulations dramatically decrease the total number of loci found to be under selection compared with traditional tests.

they observed allele frequencies that arose quickly in one environment that then decreased in frequency in the new environment implying that alleles that were beneficial in one environment were detrimental in the other (i.e., antagonistic pleiotropy across environments, Figure 4). Nevertheless, trade-offs across environments are far from universal: In another experiment when yeast were exposed to fluctuating selection, they occasionally evolved generalist phenotypes that were able to outcompete specialists in both environments (Fasanello et al. 2024).

Incorporating genomic tools into experimental evolution studies can increase our understanding of observed trade-offs and provide insight into the genomic mechanisms at play in fluctuating and multistressor environments. For example, a clear trade-off between survival and growth was observed for purple sea urchin larvae exposed to fluctuating pH conditions in contrast to static low pH conditions, but the same loci were found to be responding to both selection regimes, indicative of a shared genetic basis underlying survival across fluctuating vs. static pH conditions (Garrett et al. 2020). The authors found that allele frequency changes were in the same direction across selection regimes, suggesting there is no genetic trade-off for adaptation to either fluctuating or static low pH exposure. In contrast, adaptation to extreme low pH conditions targeted a unique set of loci, suggesting that survival under these conditions is genetically uncoupled from survival at less extreme low pH and fluctuating conditions. Whether adaptation to extreme conditions leads to trade-offs in other conditions is still unknown.

The genomic response to single versus multistressor selection experiments can also reveal surprising patterns of trait correlation. In a copepod exposed to 25 generations of selection, 37% of the genomic response was shared among the single stressor (warming only) and the multistressor exposure (warming and acidification). Even more surprisingly, only 1% of the allelic response was shared among a different single stressor (acidification only) and the multistressor (warming and acidification), suggesting that the genomic mechanism of adaptation to multistressors is not a simple additive response (Brennan, et al. 2022a).

Experimental evolution and resequencing techniques have yielded important mechanistic insights into the process of adaptation, including, the functional annotation of genes undergoing expression changes during evolution (Brennan, et al. 2022a;

BOX 3 | Plasticity and plasticity-tolerance trade-offs: a common and important outcome of experimental evolution studies involving climate change and anthropogenic stressors.

A commonly observed trade-off during experimental evolution in the context of climate adaptation is a loss of tolerance plasticity with increases in mean tolerance (Brennan, et al. 2022a; Brennan et al. 2019; Demayo et al. 2021; Morgan et al. 2020; Sasaki and Dam 2021; Figures 2b and 3). Trait plasticity is an important mechanism for persistence in a variable environment, which may allow individuals to persist long enough for genetic assimilation and adaptation to occur (Levis and Pfennig 2016; Snell-Rood and Ehlman 2021). However, selection may act on plasticity itself promoting acclimatization strategies rather than a canalization of tolerance limits (Kelly 2019; Wund 2012) causing a trade-off between plasticity and evolution of increased maximum tolerance in natural populations (Tikhonov, Kachru, and Fisher 2020). Therefore, in cases where populations do evolve increased tolerance, this may not necessarily reduce vulnerability to climate change, if increased tolerance comes at the expense of plasticity (Barley et al. 2021; Kelly et al. 2017).

Despite the key insights that measuring plasticity trade-offs can provide, few experimental evolution studies have incorporated measurements of plasticity alongside mean tolerance. One reason may be that the typical experimental approach to measuring plasticity in experimental evolution populations uses a split-brood or hardening approach, which involves measuring tolerance not only across multiple generations, but also in groups acclimated to different conditions (essentially doubling the number of individuals and the amount of experimental effort required). Furthermore, this approach can be vulnerable to the statistical artifact known as regression to the mean (Gunderson 2023; Kelly and Price 2005), which can be remedied through design changes, but these further increase the number of experimental units required (Gunderson and Revell 2022).

While these additions increase the experimental effort and difficulty, the insights gained from not only identifying plasticity-tolerance trade-offs, but examining how these trade-offs may themselves evolve, are essential for a full understanding of population responses to climate change and anthropogenic stressors. Like changes in mean tolerance, plasticity can be examined from both a phenotypic and genomic perspective. For example, multiple studies in marine copepods found a loss of transcriptional plasticity following multiple generations of selection, demonstrating a direct link between a loss of plasticity at the phenotypic and molecular level (Brennan, et al. 2022b; Kelly et al. 2017). Investigating plasticity trade-offs offers an exciting, important, but complex addition to the experimental evolution repertoire.

Hsu et al. 2021), the distribution of polymorphisms under selection in the laboratory versus. in the wild (Griffiths, Kawji, and Kelly 2021), and the redundant nature of polygenic traits under selection (Barghi et al. 2019; Láruson, Yeaman, and Lotterhos 2020). Nevertheless, several caveats are warranted when seeking to use genomic data to understand responses to experimental selection which we have outlined in Box 2.

Glossary

Evolutionary Rescue: Populations escape extinction in stressful or deleterious conditions through adaptation via natural selection.

Experimental Evolution: Populations of organisms are exposed to a set of conditions in the laboratory over multiple generations in order to measure their evolutionary responses.

Trade-Off: One trait is constrained by another such that when one trait increases the other must decrease.

Tolerance: The maximum capacity of an organism to persist when exposed to a given stressor. For example, the thermal maximum of an individual or the lethal concentration of a pollutant.

Plasticity: The ability of a given genotype to produce different phenotypes in response to the environment. In the context of stress responses, this often involves the ability of an organism to increase their tolerance to a stressor after an initial, sublethal exposure when encountering that stressor again (see Box 3).

Energetic Trade-Off: Organisms must delegate a finite number of resources to multiple metabolic, functional, and life history processes that may force trade-offs between different traits.

Genetic Trade-Off: Traits may become negatively correlated due to either pleiotropy or linkage disequilibrium and therefore cannot be selected for simultaneously.

Genome-Wide Association Analysis (GWAS): Association test between a phenotypic trait of interest and the causative loci/SNPs.

Genomic Prediction Models (GPM): Uses identified loci from GWAS to predict unmeasured traits in an unknown environment.

The genomic architecture of adaptation has also been characterized with other types of genome scans, such as *Genome-Wide Association Studies (GWAS)* and *Genomic Prediction Models (GPM)*. In contrast to experimental evolution, phenotypic traits for current populations (as opposed to artificially evolved) are associated with standing genetic variation (Capblancq et al. 2020), but these analyses can require extremely large sample sizes to have enough statistical power to detect historical signatures of selection and loci with small-effect sizes (Barton 2022). These methods have yielded important insights into the genetic variants associated with human diseases (van der Sijde, Ng, and Fu 2014; Tam et al. 2019), the genetic improvement of agricultural crop and animal breeding (Crossa et al. 2021; Romero Navarro et al. 2017; Fradgley et al. 2023), and more recently identifying ecologically relevant adaptive traits in nonmodel organisms (Fuller et al. 2020; Enbody et al. 2022; Capblancq et al. 2020). These methods can also be used to determine if correlated traits are also genetically correlated with either pleiotropy or linkage disequilibrium or whether each trait has an independent genetic basis (Korte et al. 2012; Santure and

Garant 2018). For example, positively correlated body size traits in polar bears have been mapped to a single locus and show potential to be acted upon by selection (Malenfant et al. 2018), whereas genetic constraints for wing pattern evolution have been identified in *Lycaeides* butterflies (Lucas, Nice, and Gompert 2018). GWAS or GPM approach may be more appropriate than experimental evolution for species with long generation times or species that are not amenable to lab/captive environments. However, these approaches may not be able to accurately model how trade-offs will interact and evolve in future/unknown environments (Hoffmann, Weeks, and Sgrò 2021). The benefits and disadvantages for each experimental method must be carefully considered based on the researcher's question and the biology of their system (Shaw 2019; Hoffmann, Weeks, and Sgrò 2021).

4 | Environmental Context and Selection Regime

Whether trait correlations are generated by pleiotropy or limited resources, the realization of a trade-off will depend on the selection environment. If two traits are positively correlated, this will only result in a trade-off if natural selection favors larger values of one trait and smaller values of the other, but the trait correlation will actually enhance the effects of natural selection if selection favors larger values for both. Additionally, adaptation to one stressor, such as heat, may also result in reduced tolerance to other stressors, such as pollutants (Moe et al. 2013; Figure 3). However, the negative correlation between tolerance of heat and tolerance of pollution will only result in a trade-off if organisms are simultaneously under selection for increased tolerance of both heat and pollution. In laboratory selection experiments of model organisms, new mutations often appear to be trade-off free (improving fitness across multiple traits) and trade-offs are only revealed across denser sampling regime of traits and environments (Li, Petrov, and Sherlock 2019). Finally, pleiotropy may be hard to predict in environments that are distant from the one in which an allele was initially favored (Kinsler, Geiler-Samerotte, and Petrov 2020), emphasizing the importance of careful selection of environments in which to test experimental lines.

Stressors typically co-occur and fluctuate in intensity in the wild, unlike the static exposure regimes used in many laboratory selection experiments. This is an important consideration given that many studies have found important differences in fitness under fluctuating environments relative to static conditions (Dufault et al. 2012; Frieder et al. 2014; Jarrold et al. 2017; Rescan et al. 2021). For example, purple sea urchins exposed to static low pH, larvae exhibited decreased survival and growth. However, under fluctuating low pH selection, larvae were even smaller in size, but exhibited reduced mortality, suggesting a potential trade-off between survival and growth (Garrett et al. 2020). Other studies have observed less severe fitness trade-offs under fluctuating conditions as opposed to extreme static conditions, possibly due to the temporary restoration of less stressful conditions (Schaum et al. 2018). In comparison, some studies find that exposure to multiple stressors often dampens the response to selection compared to single stressors (Orr et al. 2022), potentially due to trade-offs. For the monocot grass, *Phragmites australis*, experimental selection exposures in the field to increased CO₂ and N abundance resulted in trade-offs where plants could adapt to either stressor in isolation, but not both (Mozdzer

et al. 2022). Fluctuating environmental conditions also often promote the evolution of plasticity as an adaptive strategy (King and Hadfield 2019; Pfennig 2021), which may incur its own set of trade-offs (Box 3).

Although the quantification of trade-offs depends on experimental design, conditions in the laboratory are often a poor representation of how selection will operate in the wild (Biselli, Schink, and Gerland 2020; Burny et al. 2022). Exposure to a single static stressor may find that a species has a high capacity for adaptation, but trade-offs may be revealed under multistressor conditions that also naturally occur in the wild (Dam et al. 2021; Langer et al. 2019; Orr et al. 2022). For example, under warming conditions alone, copepods were able to recover fitness after 25 generations, while this recovery was limited under combined warming and acidification stressors (Demayo et al. 2021). Responses to selection may also be altered by prior histories of adaptation to other stressors. For example, *Drosophila melanogaster* with a prior history of interspecific competition evolved faster development times and lower fecundity when subsequently exposed to experimental selection for adaptation to cooler conditions (Grainger and Levine 2022). The occurrence of trade-offs may also depend on the magnitude and duration of the stress exposure, with trade-offs becoming less detectable with slower and lower selection regimes (Santos et al. 2023). In *Drosophila subobscura*, while both the fast and slow ramping selection protocols achieved similar evolutionary responses in CT_{max} (critical thermal maximum, a common measure of thermal tolerance), only the fast-ramping protocols resulted in trade-offs. Faster ramping rates resulted in an increase in thermal optimum, but came at the cost of a decrease in thermal breadth, while the slow ramping protocol left the remainder of the thermal performance curve unchanged (Mesas, Jaramillo, and Castañeda 2021). The choice of which trait will be the primary target of selection matters. In *Drosophila*, selection for increased starvation tolerance led to decreased cold tolerance, but selection for increased cold tolerance did not produce a similar decrease in starvation tolerance (Aggarwal, Mishra, and Singh 2023).

Finally, trade-offs may be altered by selection over time, as compensatory mutations may reduce trade-offs over longer timescales. As a result, long-term selection experiments may provide a different view of trade-offs than those observed during the initial generations of an experiment (Dam et al. 2021; Demayo et al. 2021; Jin et al. 2022). Additionally, populations spending long time spans and many generations in the laboratory may adapt to these artificial conditions. Therefore, making careful comparisons of evolutionary change across control groups and treatment groups at the beginning and end of the experiment is essential to fully measure the genomic adaptation to the stressor of interest (Box 2; Brennan, et al. 2022a; Hoffmann, Sgro, and van Heerwaarden 2023). All of these examples highlight the caution that is warranted when using single-stressor selection experiments over limited generational timescales to predict responses to multidimensional climate change.

5 | Conclusion

It was once thought that the time scale of evolutionary change was too long for evolutionary rescue to play a consequential role

in ecological responses to contemporary environmental change. We now appreciate that evolution can occur rapidly enough to influence responses to climate change, but the magnitude of these influences is still unknown. Challenges remain, but by quantifying the genomic architecture of key traits and identifying the trade-offs incurred by climate adaptation, experimental evolution studies are poised to play a key role, not just in identifying the capacity for adaptation, but for helping us to understand the consequences of evolutionary responses to climate change, where and when they occur.

Author Contributions

Joanna S. Griffiths: conceptualization, writing – original draft, writing – review and editing. **Matthew Sasaki:** conceptualization, writing – original draft, writing – review and editing. **Isabelle P. Neylan:** writing – original draft, writing – review and editing. **Morgan W. Kelly:** conceptualization, writing – original draft, writing – review and editing.

Conflicts of Interest

The authors declare no conflicts 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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Supporting Information

Additional supporting information can be found online in the Supporting Information section.