



Within- and Trans-Generational Environmental Adaptation to Climate Change: Perspectives and New Challenges

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The current and projected impacts of climate change are shaped by unprecedented rates of change in environmental conditions. These changes likely mismatch the existing coping capacities of organisms within-generations and impose challenges for population resilience across generations. To better understand the impacts of projected scenarios of climate change on organismal fitness and population maintenance, it is crucial to consider and integrate the proximate sources of variability of plastic and adaptive responses to environmental change in future empirical approaches. Here we explore the implications of considering: (a) the variability in different time-scale events of climate change; (b) the variability in plastic responses from embryonic to adult developmental stages; (c) the importance of considering the species life-history traits; and (d) the influence of trans-generational effects for individual survival and population maintenance. Finally, we posit a list of future challenges with questions and approaches that will help to elucidate knowledge gaps, to better inform conservation and management actions in preserving ecosystems and biodiversity.

Keywords: climate fluctuation, evolution, developmental plasticity, trans-generational effects, adaptation, life-history trait

INTRODUCTION

Global climate change is projected to continue modifying environmental conditions at unprecedented rates (Lüthi et al., 2008; IPCC, 2014). These changes have dramatic consequences for ecosystems and communities by reducing species abundance and in extreme cases causing species extinction (Thomas et al., 2004; Willis et al., 2008; Hoffmann and Sgrò, 2011), leading to decreased biodiversity (Parmesan and Yohe, 2003; Landman et al., 2005; Burlakova et al., 2014; Zhang et al., 2018). In aquatic systems, the effects of climate change include, among others, fluctuations in oxygen availability, increased acidification, and extreme stochastic temperature events (Caldeira and Wickett, 2005; IPCC, 2014; Jenny et al., 2016; Dahlke et al., 2020). The magnitude, duration, and periodicity of these changes likely mismatch the existing evolved coping capacities of species, compromising population maintenance and resilience (Johansen et al., 2021). Mitigation of the effects of climate change can take place within and across generations. Within-generational mitigation can occur through relocation to more favorable environments (Pinsky et al., 2013). However, when relocation is not feasible, within-generational mitigation can then

occur through individual acclimatization by phenotypic plasticity (Crozier and Hutchings, 2014). If individuals of a population survive and are able to reproduce, the effects of climate change can then be attenuated across generations via non-genetic inheritance or genetic adaptation (Gienapp et al., 2008; Andrewartha and Burggren, 2012; Ryu et al., 2020).

To better understand the impacts of projected scenarios of climate change on individual fitness, population maintenance, and species resilience, it is thus crucial to frame future experimental studies under an integrative approach that considers how the proximate environmental causes of individual variability that affect plastic responses can influence the ultimate functional and potential adaptive responses to environmental change. As the number of studies on climate change increases, the complexity of its effects becomes more evident. In fact, these advances bring along new challenges for the scientific community, such as providing more ecologically relevant predictions that integrate natural-field conditions in experimental designs while overcoming technological and logistic constraints.

In this perspective we focus on aquatic systems to first highlight the importance of considering different time scales of fluctuations in environmental conditions, for example, comparing the effects of short-term variations (i.e., daily fluctuations) to long-term projected scenarios (i.e., average changes of climate change). Second, depending on the environmental condition, the organismal physiological capacities to cope with disturbances partially depend on the “maturity” of its organs and systems. Therefore, variability in plastic responses to environmental challenges within a population will likely arise based on the organism’s developmental stage. Third, species’ life history traits (e.g., life span, generational time, and reproductive strategy) rely on the availability of resources through time and location. However, variability within and across habitats imposes challenges on fitness. Thus, it becomes important to determine how climatic variability will impact life history traits, as well as to determine if the response to these challenges will be similar across species with different life histories. Fourth, we discuss how within-generational responses to fluctuations in environmental conditions can affect the phenotype of subsequent offspring generations, and potentially induce genetic adaptation. Finally, we list potential directions for future experimental studies that will provide more realistic predictions of the consequences of climate change on populations.

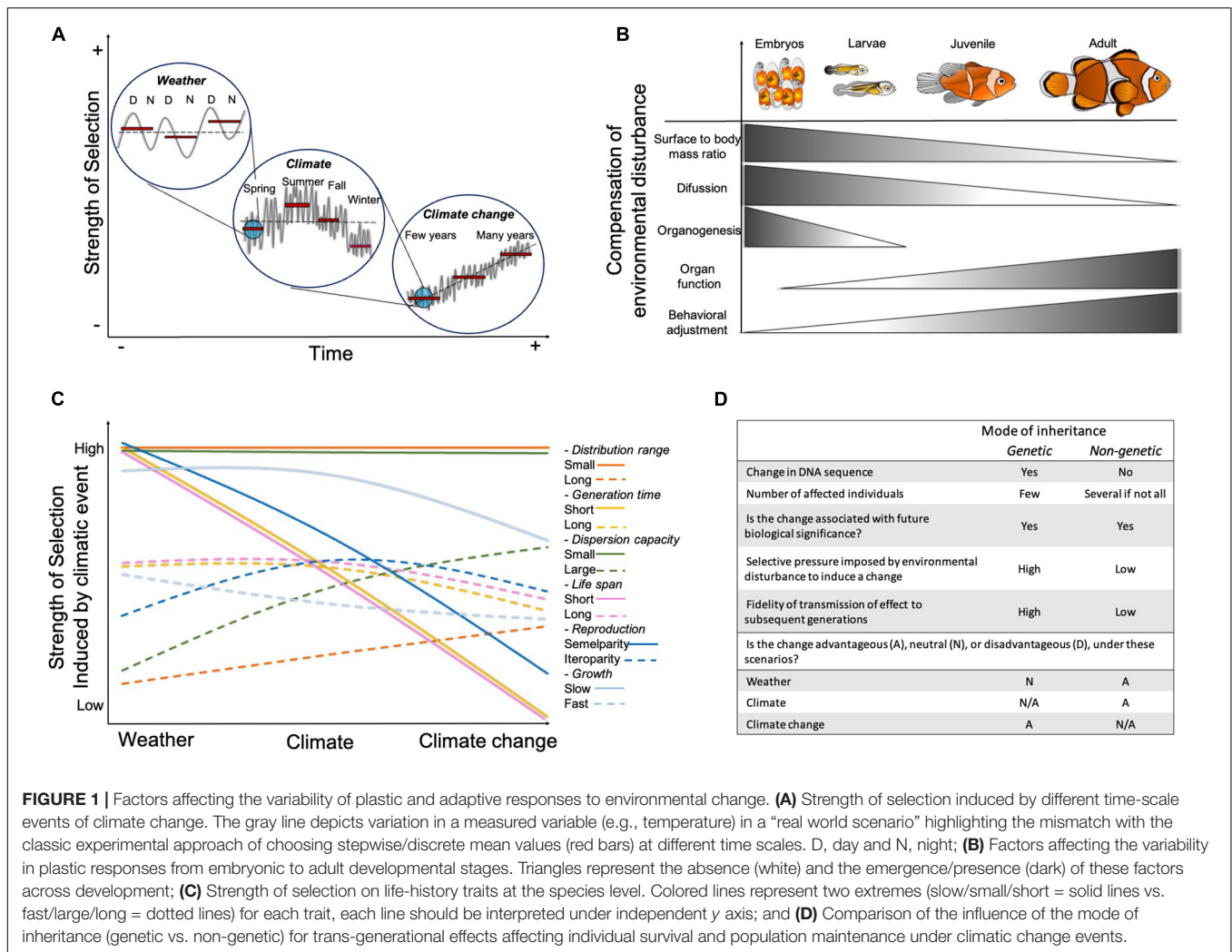
TIME-SCALE EVENTS: WEATHER, CLIMATE, AND CLIMATE CHANGE

Climate change refers to significant long-term changes in average environmental conditions. These changes include, among others, modifications of temperature cycles, carbon dioxide and oxygen levels, pH of water, precipitation, and wind patterns (Burroughs, 2007; Bopp et al., 2013). Although these variables fluctuate naturally and impose constant challenging conditions for individuals and populations, their occurrence, variability, amplitude, and unpredictability have been exacerbated since

the industrial revolution (Jenny et al., 2016; Johansen et al., 2021; **Figure 1A**). Strikingly, most of the studies aimed at understanding the effects of climate change consider discrete stepwise changes of a selected “stressor” that reflect the mean values of long-term predicted scenarios. Commonly, after exposing the study species to the new steady level, a description of the organismal (or population) responses and speculations about their adaptive capacity are provided (e.g., Rosa et al., 2014; Rummer et al., 2014; Dixon et al., 2015; Faria et al., 2018; Johansen et al., 2021). For example, studies investigating the effects of global warming and ocean acidification generally expose the individuals to a constant + 3°C or – 0.3 pH units, respectively, before assessing individual fitness related traits, such as growth and survival (Sheppard-Brennand et al., 2010; McLeod et al., 2013; Rasconi et al., 2015; Crespel et al., 2017; Qui-Minet et al., 2019). However, in nature, ambient conditions rarely, if ever, change in a stepwise fashion, and organisms face fluctuations in environmental conditions at time scales of hours, days, months, and years (Burggren, 2018). Recent studies have highlighted that the responses of individuals within a population will vary when exposed to a constant or fluctuating conditions (Drake et al., 2017; Hannan et al., 2020). Therefore, to better understand the impacts of climate change on organisms and populations, it is necessary to integrate more naturally relevant variability of environmental conditions in experimental designs and to differentiate the effects of stochastic *weather* events –short-term every day and weekly changes in ambient conditions– from those of *climate* –seasonal and yearly changes in ambient conditions– and *climate change* –predicted changes in mean values of environmental parameters across decades and centuries– (Burroughs, 2007; **Figure 1A**).

Habitats vary in their capacities for buffering changes in environmental conditions (Malhi et al., 2020), and their resident species reflect this variation. Nonetheless, even if organisms are physiologically able to cope with the environmental stress imposed by a single extreme event (e.g., heat waves), it is possible that repeated and long-term exposure to unpredictable conditions will likely outweigh their existing evolved coping capacities (Le Nohaïc et al., 2017; Johansen et al., 2021)–compromising survival and contribution to future generations. For example, thermally resistant corals from Northwestern Australia that have been able to thrive in daily temperatures up to 37°C, experienced severe mass bleaching (<80.6%) in 2016 due to extreme heatwaves of 4.5–9.3° heating weeks for about 5 months (Le Nohaïc et al., 2017). This study highlights the importance of considering both, stochastic extreme weather events as well as medium- and long-term natural climatic variability in experimental designs.

Noteworthy is the fact that the combination of environmental stressors –which is the norm more than the exception in nature– can have antagonistic, additive or synergistic effects on organisms and populations (Darling and Côté, 2008; Lefevre, 2016; Montgomery et al., 2019). For example, oxygen consumption of marine ectotherms is more commonly affected by additive or antagonistic interactions between ocean warming and acidification than by a synergistic effect (see Lefevre, 2016; Pistevo et al., 2016; Leo et al., 2017). Consequently, the empirical



consideration of multi-stressor interactions will render a better understanding of the effects of climate change.

VARIABILITY IN PLASTIC RESPONSES WITHIN A GENERATION

Developmental Stage

Individual plastic responses to weather and climate events are expected to vary across developmental stages. Embryonic and larval stages are considered to be more sensitive to variable environmental conditions in comparison to adult stages, because of reduced plastic capacity (Burggren and Bautista, 2019; Dahlke et al., 2020). Inherent to early development is the progressive maturing of rudimentary morphological structures and physiological functions that allow organisms to regulate homeostatic disturbances (Figure 1B). In fish for example, as development progresses and the surface to body mass ratio decreases, homeostatic regulation by diffusion through skin is gradually replaced by the interrelated functions of the forming organ systems (Rombough, 1998, 2002; Burggren et al., 2017).

During organogenesis, disturbances induced by challenging environmental conditions can compromise the survival of early life stages (Réalis-Doyelle et al., 2016). However, if they survive, the effects can remain present later in life potentially compromising metabolic rates, reproduction, and population replenishment (Jonsson and Jonsson, 2014; Durtsche et al., 2021). In contrast, the experience of environmental challenges early in life can also have positive phenotypic effects. For example, improvement of skeletal development (faster mineralization) was reported in larvae of the seabass exposed to hypercapnic conditions (Crespel et al., 2017). Worth mentioning is the fact that early exposures in life can also lead to positive effects in later developmental stages and not only at the exposed stage (Gobler and Talmage, 2013; Vanderplancke et al., 2015; Spinks et al., 2019). For instance, zebrafish embryos incubated up to hatching in colder or warmer temperatures, exhibited improved swimming performance as adults when exposed to temperatures resembling their temperature of incubation (Scott and Johnston, 2012). However, to date we still have poor understanding of the plastic capacities at the whole organismal level in developing organisms (e.g., thermal limits and tolerance

ranges), as well as of the actual partitioning of their regulatory mechanisms in organ and systems (e.g., acid-base regulation), and the potential trade-offs with other traits, when facing environmental disturbances (West-Eberhard, 2003; Burggren and Bautista, 2019). This lack of knowledge mainly arises from the intrinsic complexity of studying the effects of climate change in tiny sized organisms, and the inherent technological challenge of developing and implementing reproducible techniques for such specialized measurements.

Although adult life stages exhibit well established physiological acid-base and thermoregulatory capacities, as well as the capacity for adjusting their behavior in response to their surrounding environment, their plasticity and susceptibility to environmental disturbances can vary depending on their reproductive status. Indeed, scenario-based projections of climate change suggest that spawning adults have significantly narrower thermal tolerances (Dahlke et al., 2020). In addition, environmental variation can induce alteration in neuroendocrine pathways, modifying metabolism, disrupting homeostasis and exacerbating production of reactive oxygen species, leading to acceleration of development and aging (Burraco et al., 2020). Therefore, different developmental stages are likely to respond to stressors through distinct mechanisms and with different sensitivity and plasticity. Because populations are composed of individuals of different developmental stages, a particular sensitivity or lack of plasticity in one of the stages may lead to the collapse of the entire population. Therefore, investigating the effects of weather and climate events in all developmental life stages is crucial to provide more reliable information on how populations could be affected by future conditions (Figure 1B).

Life History Traits

Availability of resources varies with seasonality and across habitats with different environmental conditions. Furthermore, organisms' life history traits represent how variable the environmental changes are in their habitat (Hovel et al., 2017; Chaparro-Pedraza and de Roos, 2019). Consequently, changes in the species geographic distribution and its realized niche induced by climate variability can impact these traits (de Roos and Persson, 2013; Wang et al., 2020; Chaudhary et al., 2021). For example, the reproductive strategies of the majority of species depend on environmental conditions (e.g., temperature, salinity, light:dark cycles, and food availability). Therefore, a delay or acceleration in the timing for reproduction in semelparous species -characterized by death after first reproduction- can lead to a phenological mismatch between larval exogenous feeding and food availability (Durant et al., 2007; Renner and Zohner, 2018), increasing mortality and compromising effective population size (Figure 1C). In comparison, iteroparous species -with multiple reproduction events in their lifetime- may be more capable of buffering the effects of climate variability by regulating parental investment across their clutches (Parker, 2002; Cayuela et al., 2014), although long-term and recurrent scenarios may still threaten population recruitment. Therefore, as different species perceive the changes in environmental conditions depending on the granularity of the habitat that they inhabit (Levins, 1968; van Tienderen, 1991, 1997), it becomes necessary to consider the

species' dispersal needs and capacities as well as their migration patterns -if present- when interpreting results from experimental studies (Figure 1C).

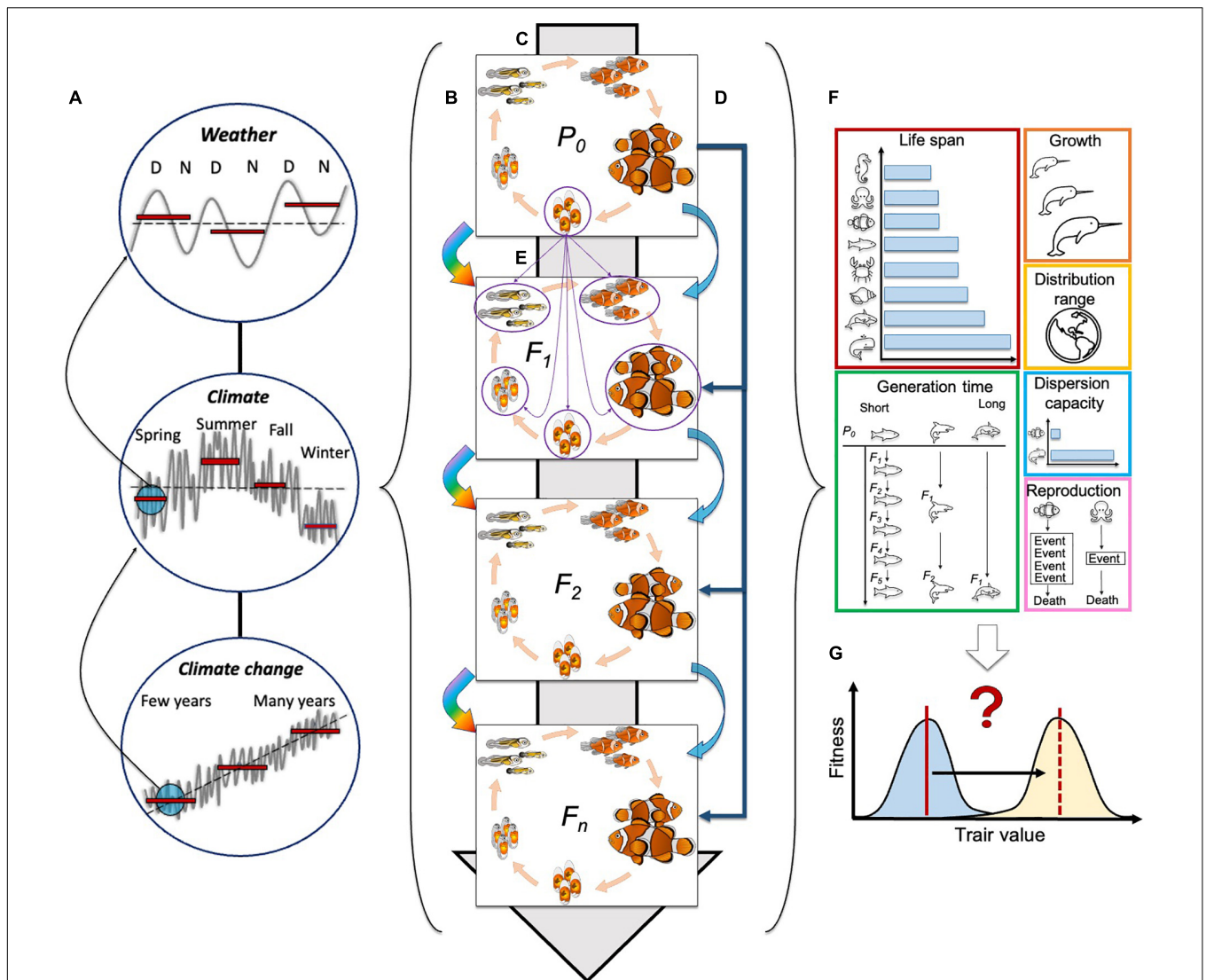
The effects of climate change can also affect species differentially based on their lifespan and generation time. For example, in comparison to taxa with short-generation times (benthopelagic and reef fishes; up to 5 years), accelerated development and life histories due to global warming can lead to lower mortality and higher fecundity earlier in life in taxa with long-generation times (elasmobranch, bathydemersal, demersal; over 10 years) (Wang et al., 2020). In addition, simulation models suggest that species that possess long lifespans, relative to the change in environmental conditions, may be more plastic in comparison to species with short lifespan (Ratikainen and Kokkoo, 2020). Overall, the differential responses related to lifespan and generational time of a particular species will induce inter- and trans-generational effects that will affect the number of generations experiencing climate variability as well as the species potential for evolutionary adaptation (Figure 1C).

BEYOND A SINGLE GENERATION: TRANS-GENERATIONAL ACCLIMATION AND ADAPTATION

Evolutionary Adaptation

Within-generational phenotypic plasticity allows organisms to face the challenges directly imposed by variable environmental conditions. However, to persist in the long-term, populations must cope with the continuous environmental challenges through adaptation across generations. Adaptation occurs through genetic inheritance, i.e., evolution (McGuigan et al., 2021; Figure 1D). For evolution (genetic adaptation) to occur, empirical evidence must demonstrate that the environmental fluctuations due to climate change can lead to modifications in genetic sequences, and that these changes are the result of natural selection (Merilä and Hendry, 2014; Ehrenreich and Pfennig, 2016). The new environmental pressures are likely to induce selection on specific fitness-related traits, resulting in the shift of the allele frequencies of these traits across generations (Bernatchez, 2016; Manhard et al., 2017). Micro evolutionary changes can occur across a small number of generations and at ecological relevant timescales (Hairston et al., 2005; Carroll et al., 2007; Bell and Aguirre, 2013; Hendry et al., 2018; Reznick et al., 2019). However, the species' evolutionary potential may still be low when the rate of change in the environmental conditions outpaces the rate of the species adaptation. For example, a recent study on thermal tolerance in zebrafish artificially selected over six generations to increase or decrease their upper thermal tolerance, reported that these fish exhibited a slow rate of adaptation compared to the rate of global warming, suggesting that such tropical species may meet adaptive constraints when facing global warming (Morgan et al., 2020).

Taken together these studies highlight the need for determining whether adaptation from existing genetic variation



within populations would be sufficient to cope with the rate of change of climatic variables.

Non-genetic Inheritance

The adaptability of future generations to fluctuating environments can also be influenced by non-genetic inheritance

and can happen from one generation to the next (Ezard et al., 2014; Ryu et al., 2018; Bautista and Burggren, 2019; Cavieres et al., 2020). Although not completely understood, the mechanisms responsible for this type of trans-generational acclimation include, maternal provisioning, microbiome transfer, inheritance of epigenetic markers (e.g., DNA methylation,

small RNAs, and histone modifications), and behavioral and cultural processes (Bonduriansky et al., 2012; Burggren, 2016, 2018; Bonduriansky and Day, 2018; Ryu et al., 2018; Bautista et al., 2020; Jablonka and Lamb, 2020; Crespel et al., 2021). Although the role of non-genetic inheritance on adaptation and evolution is still under debate (Laland et al., 2014; Charlesworth et al., 2017), trans-generational effects can be stable and can substantially impact organisms' responses to environmental change over several generations (Ryu et al., 2018; Yin et al., 2019; Jablonka and Lamb, 2020). However, their advantages and disadvantages under the different scenarios of climate change are yet to be determined (Munday, 2014; Morgan et al., 2020; **Figure 1D**). For instance, trans-generational acclimation is particularly advantageous when the change in environmental conditions is slow, and the environmental correlation between parents and offspring is high (Munday, 2014; Uller et al., 2015; Bernal et al., 2018). However, if trans-generational acclimation moves the mean of the phenotype of interest closer to the fitness optima imposed by the environmental change, the strength of selection may be weakened because individuals with different genotypes but with similar phenotypes -induced by non-genetic mechanisms- may exhibit similar fitness (Falconer and Mackay, 1981; Price et al., 2003; Ghilambor et al., 2007; Wild and Traulsen, 2007). Consequently, the rate of genetic adaptation will likely be slowed down (Huey et al., 2009; Donelson et al., 2019), or it can be eliminated in extreme cases (Price et al., 2003). Therefore, more research is still needed to understand this phenomenon and to determine if its buffering capacity would last long enough across generations to lead to genomic fixation (e.g., genetic assimilation). Nonetheless, modeling suggests that when selection acts on genetic and non-genetic mechanisms in the same systems, adaptation takes place at a faster rate than in systems where selection acts just on one mechanism (Klironomos et al., 2013).

FUTURE CHALLENGES AND APPROACHES

Finally, we propose a list of future challenges that can help to elucidate knowledge gaps and better predict, validate, and inform conservation and management actions to preserve ecosystems and biodiversity. Therefore, with this perspective we advocate for future studies to focus on describing the evolutionary implications of the interaction between within- and trans-generational responses to climatic events. The inherent complexity of understanding the effects of climate change -at any of its scales- also highlights the need for interdisciplinary efforts among the scientific community (see **Figure 2**).

Challenge 1: To integrate more realistic and naturally relevant variability of environmental conditions in experimental designs (e.g., stochasticity, daily, or seasonal cycles).

- Include more variability, unpredictable frequency, magnitude, and amplitude of fluctuations in environmental conditions.

- Differentiate the specific effects of weather, climate and climate change events on individual fitness-related traits.
- Consider the interaction between multiple stressors in experimental designs at all scales.

Recommendation: By positioning data loggers in the field, researchers can find information about the magnitude and frequency of natural environmental fluctuations. This information may be also found in public data bases. Microcontrollers (e.g., Arduino, see Drake et al., 2017) or timers can be used on temperature or gas control devices to recreate the fluctuations in experiments. Exposing the studied organisms for different length of time to these conditions will then help to distinguish the impacts of the different climatic events. Furthermore, the recreation of environmental conditions reflecting the interactions between at least two relevant environmental stressors for the organisms (for example among temperature, hypercapnia, hypoxia, pH, and salinity) can be used to provide even more accurate predictions.

Challenge 2: To characterize the effects of climatic events on plastic responses from the cellular to the whole individual level at different developmental stages (embryos, larvae, juveniles, adults, and reproductive adults).

- Document the range of plastic response at the different developmental stages within a population.
- Determine what is the actual partitioning of the roles of specific organs and systems for coping with climatic events as the organism develop.
- Determine the consequences of exposure to climatic events during early life stages for overall species fitness.

Recommendation: For experiments on early development, studies must be guided by specific developmental processes and not by "chronological development." Some things to consider are, for example, when organogenesis or metamorphosis occurs. The use of model species to produce specific knock-out organisms would help to determine the role of specific organs and systems. Experiments on adults could compare the plastic response before, during or after the breeding period in iteroparous species, or at least mention the reproductive status of the individuals under study. Although we acknowledge that there might be technological constraints, we advocate for applying the August Krogh's principle for choosing the right species model to answer the question of interest. Furthermore, analyzing the response of juveniles or adults after an early life stage exposure would provide useful information on the carry-over effects of environmental stress on the species fitness.

Challenge 3: To determine the influence of climatic events (weather, climate, and climate change) on both: individual and combined life-history traits to elucidate its consequences for species resilience.

- Implement more studies considering life history traits to improve experimental designs and interpretation of results.
- Determine the effects of climatic events on the phenology of life history traits.

Recommendation: Studies could include several species representative of different levels across two opposite extremes of any life-history trait of choice in their design or could design and interpret an experiment based on the life history of the species under study. For example, studies will benefit from using more evolutionary approaches for short generation species while focusing on plastic responses for long generations species. In addition, studies could implement re-location of individuals in field studies (under controlled designs) using translocation approaches to see how life-history traits could be modified by the environment. Because of the inherent complexity of integrating a large number of species in these studies, these challenges may be aided by particularly in mathematical modeling.

Challenge 4: To evaluate the limits – if any – of evolutionary adaptation in response to climate change.

- Document if the genetic heterogeneity of populations will be enough to allow for adaptation and relate it with the biology of the species.
- Determine if microevolution can happen in response to climate change and if the rate would be fast enough to overcome its effects.

Recommendation: Studies could determine if future environmental conditions would be able to induce a shift of the optimum values of fitness traits and life-history traits, as well as to determine if species would be able to gradually improve these changes across generations at a rate faster than climate change. Studies could also compare the evolutionary potential of different populations depending on the level of their genetic background or previous experience to new fluctuating environments (e.g., because of geothermal activity). The difference in the genetic basis of the populations either exposed or not could also be evaluated for each generation. This approach will render more precise documentation of the potential and rate of microevolutionary changes. In addition, these experiments would provide even more accurate predictions by including populations composed of individuals at different developmental stages.

Challenge 5: To estimate the limitations and scope (buffering capacities) that trans-generational effects have for species resilience under climatic scenarios.

- Determine the importance of non-genetic inheritance for overcoming environmental challenges, across several generations, by investigating the interaction between within- and trans-generational responses and the specific mechanisms of inheritance.

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- Determine how the within generational response of a population can improve or limit the response of future generations.
- Unravel the interplay between genetic and non-genetic molecular basis of physiological, and behavioral responses that help organisms to cope with climatic events, and if these mechanisms can lead to genetic assimilation.

Recommendation: Studies could determine if populations exposed to new environmental challenges are able to adjust their phenotype, transfer it and improve, or limit the response of their offspring over several generations by using common garden experiments. The studies could at the same time document a variety of the different non-genetic mechanisms (for example maternal provisioning, microbiome transfer, or epigenetic markers) to relate to the phenotypic adjustments. Genetic sequencing can also be used in parallel of epigenetic sequencing, to determine if the sequences under epigenetic regulation in one generation match the sequences under genetic evolution in later generations and how those sequences are involved in further non-genetic mechanisms.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

NB and AC contributed for conceptualization, manuscript drafting, figure preparation, editing, and revision. Both authors approved the manuscript for submission.

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