EDITORIAL

Understanding climate change response in the age of genomics

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1 | GENOMIC APPROACHES TO EVALUATE THE IMPACTS OF CLIMATE CHANGE ON ANIMALS

Climate change is rapidly transforming environments and poses a major threat to species and ecosystems world-wide (Bellard et al., 2012; Parmesan & Yohe, 2003). Given the current levels of sustained greenhouse gas emissions (Pörtner et al., 2022; Trisos et al., 2020), climate change is predicted to be a primary cause of biodiversity loss, with an abrupt disruption of major ecological assemblages expected in the next few decades,. Even if emissions were to be dramatically reduced, it is estimated that up to 5% of all species are still at the risk of extinction from a 2°C global increase in temperature alone (Waldvogel et al., 2020). Thus, understanding how animal populations respond to these changing environments is crucial for informing conservation and mitigation strategies.

Until recently, many studies predicting animal population responses to climate change have relied on ecological niche modelling and species distribution models (Holt, 2009; Thuiller et al., 2019). However, such predictions generally assume that species' ecological niches remain constant over time and do not account for population variation or the potential for evolution (Aguirre-Liguori et al., 2021; Román-Palacios & Wiens, 2020). It is now becoming increasingly affordable to generate data at the genome and population-wide scales for almost any species (Fuller & Wellenreuther, 2022). By integrating genomic data with environmental and population data, recent studies have begun to shed light on the underlying genomic mechanisms and eco-evolutionary processes by which animal populations respond to climate change and how these populations themselves are shaped by the changing fitness landscape.

This Special Feature highlights how emerging genomic approaches are used to understand population responses to climate change across a diverse range of animal systems. Together, the set of articles contained in this Special Feature demonstrate how genomic-based approaches can be used to understand range shifts, phenotypic plasticity and local adaptation of animal populations in response to a warming climate. The contributions represent cutting-edge methods and outline future multi-omic approaches, combining different data sources (e.g. transcriptomics, analysis of structural variation and epigenetics) that go beyond single nucleotide polymorphisms (SNPs). In this Editorial, we first summarise traditional challenges in understanding the responses of animal populations to climate change and how the current era of genomic-based approaches provides exciting opportunities to address them. Next, we give an overview of the empirical contributions of this Special Feature and how they fit into a framework of best practices and guidelines for future research. Finally, we discuss the future outlook of genomic approaches to understand and predict population-level responses and call for efforts to connect these new understandings with their ecological implications to inform mitigation and conservation plans.

2 | PAST CHALLENGES AND CURRENT OPPORTUNITIES

The negative impacts of climate change on populations of vulnerable species are now incontrovertible. Evidence is accumulating that increasingly severe weather events, such as droughts and heat waves, have taken their toll on many species either directly or indirectly

through altered community dynamics (Casadevall, 2020; Iknayan & Beissinger, 2018; Sinervo et al., 2010). Despite clear evidence of climate change impacts, the research community has struggled to generalise these impacts, to generate meaningful predictions or develop anticipatory solutions. At the heart of the issue is that individual species may be able to surmount the challenges of climate change, whether (a) through range shifts to more favourable environments, (b) via phenotypic plasticity to adjust to new conditions *in situ* or (c) via adaptive changes that allow species to track changing conditions. However, the knowledge needed to predict whether a species is able to respond in these ways is often absent, with phylogenetic or trait-based analyses so far unable to predict viability and persistence in the Anthropocene.

Multi-omic approaches have the capacity to directly address this knowledge gap in our prediction and mitigation toolkit. For example, data on gene and protein expression and epigenetic mechanisms, such as DNA methylation and chromatin structure, can inform on the adaptive capacity of organisms to rapidly modify gene regulation and downstream trait expression under changing conditions. Similarly, data on standing genetic variation within populations can inform on the capacity for genetic adaptation. Finally, spatial genetic patterns among populations, such as spatial signals of gene flow, drift and adaptation, can both indicate ongoing range shifts and suggest capacity for future species movements and help to identify suitable conservation units. These technologies have the capacity to revolutionise our predictive abilities, by enabling generalisation of genomic features or loci important for climate responses across taxa, informing on spatial genetic patterns associated with species' spread or decline, and increasing our mechanistic understanding of adaptive phenotypic plasticity and its limits. Discovering such general mechanisms is currently in its infancy, but already 'omics'-based data have facilitated our ability to predict which genotypes and locations are at the greatest risk of climate change (Capblancq et al., 2020; Layton & Bradbury, 2021). Such mechanisms also hold the promise in directing our climate change adaptation initiatives, for instance, via assisted gene flow, genetic rescue, selective breeding or genetic engineering for climate resilience (Hoffmann et al., 2021; Whiteley et al., 2015).

3 | POPULATION RESPONSES TO CHANGING ENVIRONMENTS

3.1 | Range shifts

Range shifts are thought to represent adaptive responses to climate change, if changes in emigration and dispersal can enable rescue of populations from extinction in areas no longer suitable in climate or can indirectly facilitate rescue by allowing colonisation of new regions that become available beyond the former range under warming (Boeye et al., 2013). However, the rates of range shifts vary dramatically among taxa and are not well-predicted by species-level traits (MacLean & Beissinger, 2017). One reason for poor predictability is

that, while once thought of as the simple movement of individuals to track the species' climate window, range shifts are now understood as involving rapid evolutionary change (Lancaster, 2022). For example, successful range shifts often require evolution of enhanced dispersal and life histories that favour movement and colonisation. In addition, while range shifts are facilitated by changes in the climate, not all elements of the environment change at the same rate; thus most studies of range shifts suggest that some adaptation to abiotic or biotic conditions in the new range is required (Spence & Tingley, 2020). Genomic data can inform on these processes and allow researchers to better understand the mechanisms that facilitate or hinder the adaptive evolutionary processes required for successful range shifting to occur.

In this Special Feature, Moerman et al. (2021) study the genomic features underpinning laboratory adaptation during range shifts in experimental protist colonies *Tetrahymena thermophila*, specifically evaluating how environmental gradients, gene flow and sexual recombination impact the ability to adapt during a range shift. They find that sexual reproduction increases environmental adaptation relative to asexual reproduction in the absence of gene flow, but that the reverse is true in the presence of gene flow. The authors also show that genetic change occurs under all experimental range shift conditions and most often at non-coding regions (although the role of genetic hitchhiking in driving these patterns remains unclear). However, the number of inferred adaptive genomic changes was only found to be positively correlated with the changes in fitness for sexual populations, and when range shifting across a uniform environmental gradient, demonstrating that the mode of reproduction and the nature of selection each have a significant impact on the type of genetic adaptation that may occur during range shifts. This study also identified specific loci and gene functions associated with adaptation to range shift conditions; specifically, genes involved in transcription and translation, cell growth and division, and repair were found to be under selection at the range edge even under uniform conditions, consistent with theory suggesting that growth rate is under strong selection during expansion. The study by Moerman et al. highlights both the incredible power of using experimental evolution to isolate and study mechanisms and contingencies of evolution during range shifts and, as emphasised by the authors, some important limitations of such approaches, with regard to inherent biases related to the precision by which, and type of, adaptive genetic change that can be detected.

Also in this Special Feature, Dudaniec et al. (2021) study genomic changes associated with a rapidly range shifting damselfly species, *Ischnura elegans*, in Northern Europe. Specifically, they find that temperature poses a strong barrier to dispersal in both male and female *I. elegans*, which would predict a slowing of the range shift at higher latitudes where cooler temperatures are encountered. Consistent with this, the overall number of genetic migrants detected declines with latitude. However, migrants are more likely to be male at the approach of the range limit, resulting in sex differences in spatial genetic structure and male-biased sex ratios at the range limit. Males

also become larger at the expansion front, resulting in reduced sexual size dimorphism and altered patterns of sexual selection on male body size. This paper supports theory suggesting that sex-biased dispersal can alter sexual and social dynamics at the range front. Specifically in this system, larger male size favours colonisation under cooler climate regimes; however, larger males become increasingly disfavoured by sexual selection under male-biased sex ratios at the range front, suggesting that trade-offs among colonisation potential and other aspects of life history may limit range dynamics (Connallon, 2015). Earlier work by Dudaniec et al. (2018) in this system suggested that loci involved in heat tolerance, vision and ion transport are under selection at the range edge, further implicating interacting impacts of stress tolerance and mate discrimination on range dynamics.

3.2 | Plastic phenotypic responses

Species can respond to different environments by expressing different phenotypes from the same underlying genotype (Xue & Leibler, 2018). Such phenotypic plasticity is thought to be a major mechanism of response to rapid environmental change, and several examples have been described of these plastic phenotypes driving responses to global temperature increases (Bonamour et al., 2019). For example, a number of amphibian species display extreme plasticity in the timing of metamorphosis in response to habitat desiccation (Denver et al., 1998). Moreover, evidence suggests that the timing of migration in several bird species is plastic in response to warmer springs (Charmantier & Gienapp, 2014). However, it has historically been challenging to disentangle whether different phenotypic responses are the result of genetic differences between individuals or represent true plasticity (Merilä & Hendry, 2014), largely due to a lack of genomic data. In this Special Feature, Oomen and Hutchings (2022) suggest a framework for predicting climate responses based on local and regional variation in phenotypic plasticity, by combining common garden experiments to partition genetic, environmental and G×E components of transcriptomic variation across spatial scales. Recently, genomic analyses have uncovered heritable loci responsible for plasticity in response to thermal stress as well as plastic gene expression (Logan & Cox, 2020). Additionally, methodological advances have revealed a variety of epigenetic mechanisms (i.e. DNA and/or chromatin modifications that do not alter the underlying genetic sequence) responsible for plastic phenotypic responses to environmental effects, including methylation and post-translational histone modifications (Duncan et al., 2014).

In this Special Feature, Rodrigues et al. (2022) measure multiple reproductive traits of *Drosophila melanogaster* lines exposed to increasing developmental temperatures. The experiments were performed across 20 lines that were previously identified to maintain fertility regardless of the temperature at which they were raised, and 20 lines that exhibited decreased male fertility as the developmental temperature increased. By using whole-genome SNP data from these lines, the authors then identified loci contributing to intra-population variation in thermal plasticity of male fertility for the reproductive traits assayed. The genomic analyses uncover genes harbouring highly differentiated SNPs between the lines displaying differences in thermal sensitivity, and therefore reveal candidate loci associated with differences in plastic phenotypic responses to increased temperature. Several of these genes have previously been implicated to impact male fertility and stress responses in other species, which the authors suggest might plausibly demonstrate a shared genetic basis for male fertility limits. Together, these experiments and genomic analyses find genetic differentiation in the population that underlies inter-genotype variation in developmental thermal plasticity on multiple reproductive traits.

It is hypothesised that environmental changes can induce epigenetic modifications, such as gene body methylation, responsible for phenotypic plasticity. Because epigenetic modifications can be stably inherited, there is a growing interest in understanding how the epigenome may contribute to evolutionary change and physiological responses to environmental disturbances. However, as attractive as this hypothesis may be, environmentally induced epigenetic modifications are not always responsible for phenotypic changes and careful genomic analysis is required to establish an association between such epigenetic changes and physiological responses and their adaptive function. In this Special Feature, Johnson et al. (2021) use a combination of common garden experiments, Tag-seq and reduced representation bisulfite sequencing to show that differential DNA methylation has no effect on gene expression across environments in the eastern oyster *Crassostrea virginica*. The authors compared patterns of gene body methylation and global gene expression for oysters in common gardens at two sites that differed in mean salinity. While oysters from the two sites differed substantially in parasite loads, body mass and global gene expression, differential methylation was only observed at 1.4% of methylated opportunities, and there was little association between differential methylation and differential gene expression. At the same time, the authors observe pronounced variation in methylation between genetic families, demonstrating substantial statistical power of the study. The authors conclude there is little evidence that environmentally induced epigenetic modifications play a primary role in regulating transcriptomic responses to changing environments in this species.

3.3 | Evolutionary adaptation

Detecting the genomic basis of adaptation to different climatic selection regimes is an important but not a straightforward endeavour. The demonstration of selection in the wild is notoriously difficult (Endler, 2020). If selection can be demonstrated, then showing that adaptive trait differences impact fitness of individuals is the next step and requires common garden or reciprocal transplant experiments (Kawecki & Ebert, 2004). Lastly, to identify the genomic underpinnings of traits under climate selection, studies need to

identify the genomic components involved, and so further molecular research to determine the 'footprints of selection' is required as well (Ahrens et al., 2018).

Some of the contributions in this Special Feature are pioneering research to dissect the genomic underpinnings of adaptation. The contribution by Araya-Donoso et al. (2021) highlights the power of integrating physiological and morphological data to detect the impacts of selection and to unravel deep interconnections between different traits and the genome. They focus their study on the lizard *Liolaemus fuscus* inhabiting the Atacama Desert, an extreme and arid environment that constitutes a strong selective pressure on this species. To characterise features related to desert adaptation, the authors compare the desert populations to populations in the Mediterranean forests of central Chile. Trait comparisons showed that desert lizards had lower evaporative water loss and exhibited a smaller body size, different allometry, larger eyeballs and more dorsoventrally compressed heads than those from the forest, which is in line with adaptations to an arid and hot environment. Genomic analyses uncovered significant differences between lizards occupying the two environments, with 110 fixed genetic differences and 30 outlier loci located within genes. These candidate genes were associated with cellular membrane and development, and the authors suggest that these may be related to the distinct water and resource availability, and changes in habitat structure, in these environments. These findings are consistent with the growing number of studies documenting genomic variation associated with climates in reptiles (Rodríguez et al., 2017; Diele-Viegas et al., 2020; Wollenberg Valero et al., 2021). This growing number is starting to enable cross-species examinations to search for general patterns and trends in the degree of genomic reuse and functional similarity.

The contribution by Wollenberg Valero et al. (2021) utilises such accumulating datasets to apply a cross-species comparative approach in lizards. In the first step of this study, Wollenberg Valero et al. use a transcriptome dataset of 24 lacertid lizards to identify 200 genes under positive diversifying selection and associated with physiological and morphological functions. In the second part, a meta-analysis of 1100 genes under selection in vertebrate species that have adapted to different abiotic factors is performed to reveal overlapping and conserved patterns. The meta-analysis uncovered a tightly connected interactome containing many genes related to putative adaptations to climate that showed a high level of conservatism across species. Overlap between the meta-analysis dataset and the lacertid genes showed that 171 of the 200 identified lacertid genes were part of this network, highlighting their important and conserved role. This narrow panel of highly conserved candidate genes and pathways deserve concerted focus in the future research aimed at evaluating current climate stress on populations at the molecular level, and whether it may lead to evolutionary adaptation in the future in both lizards, and vertebrates more generally.

Climate adaptation in the sea, an environment that is not characterised by strong physical boundaries, is yet another topic that is being explored in this Special Feature. Many marine species, particularly those with a high dispersal ability, show low levels of genetic differentiation and large effective population sizes which together lead to low levels of genetic drift (Nielsen et al., 2009). The study by Boulanger et al. (2022) focussed on two marine finfish species in the Mediterranean Sea that show contrasting dispersal abilities: the mobile white seabream *Diplodus sargus* vs. the more movement-restricted striped red mullet *Mullus surmuletus*. Extensive spatial population sampling and genome-wide SNP markers were combined to investigate how space, dispersal and environment together shape climatic-associated genomic variation in these species. These analyses revealed contrasting patterns of gene flow and adaptive genetic variation between the two species, with the sea bream having a distinct Alboran sea population and panmixia across the Mediterranean Sea, while the mullet revealed additional differentiation within the Mediterranean Sea that linked to temperatures, as well as marine primary productivity. This is consistent with the hypothesis that restricted gene flow would facilitate the fixation of locally adapted alleles more strongly in the less mobile mullet than in the more mobile seabream. Knowledge about the interplay of movement dynamics and selection strength can help to better anticipate and mitigate future responses to climate change by allowing quantification of adaptive potentials and environmental niches of natural populations to protect vulnerable populations of a species. For example, such niche information can be used in the selection of marine protected areas (MPAs) to help maintain gene flow and allow the spread of advantageous alleles (Xuereb et al., 2020). Genomic studies provide crucial insights for designing efficient MPA networks, as they provide information on gene flow and the (mal)adaptation of populations to their changing environment. Spatial conservation planning can make use of genomic metrics (e.g. adaptive genetic diversity) to incorporate species' evolutionary potential into the design of MPA networks, by prioritising the protection of well-adapted populations.

Climate adaptation in the sea by sessile organisms is particularly intriguing, as the limited movement ability hinders many behavioural responses to cope with a warming climate that can be exploited by other, more mobile, species. The contribution by (Le Luyer et al., 2022) explores the genomic and physiological basis of individual responses to elevated temperature in the tropical bivalve species, *Pinctada margaritifera*, which has two geographic ecotypes. One of the ecotypes occupies warmer tidepools displaying large diurnal variations, while the other ecotype inhabits tidepools with stable to moderate seasonal variations characterised by lower mean temperatures. The authors sample replicate individuals of both ecotypes to illuminate both genetic divergence as well as plasticity and acclimation responses in these ecotypes to cope with habitat-specific temperature stressors. By combining lipidomic and transcriptomic approaches they find that the species' overall ability to cope with elevated temperatures is greater than that has been appreciated thus far, and that the two ecotypes appear to exploit similar physiological mechanisms to tolerate and acclimate to thermal stress, linked to the genetic variation across the populations. Intriguingly, they also detect some specific genetic and gene expression differences between the ecotypes that appear to be associated with habitat-specific thermal adaptations, particularly in the

physiological machinery associated with managing oxidative damage and mitochondrial functioning. This study as such sheds important light on how ecotypes within species may provide added intraspecific variation to the overall genetic portfolio of a species to adjust to a changing thermal regime.

As described above, the genomic era has opened up new opportunities to discover the molecular processes and genetic impact of evolution and local adaptation; however, how to correctly identify and validate true outlier loci is an ongoing debate. For natural populations with strong population structure and high genomic divergence, the detection rate of significantly differentiated loci is high. However, whether these divergent loci are caused by divergent selection or by genetic drift is difficult to determine in many cases. It is known and expected that strong population structure may affect the results of genome scans by increasing the number of false positives (Forester et al., 2018; Frichot & François, 2015; Liggins et al., 2020; Meirmans, 2012). As a consequence, applying genome scans to strongly structured natural populations requires strategies to mitigate this issue. In the contribution by Salloum et al. (2022), the authors take the advantage of a natural geographic contrast in the levels of population structure of a marine mollusc *Onithochiton neglectus*, and, thus, compare the success of genome scans in identifying adaptive loci in strong versus moderate population structure scenarios. The authors further examine the impact of connectivity levels on local adaptation, and develop a novel method to increase the probability of identifying a reliable set of candidate loci for selection. Their study supports that caution should be made when looking into highly structured populations, since these are more likely to return a higher rate of false positive loci, and that careful statistical controls (and future advancements in methodological approaches) will enable better identification of high-confidence adaptive loci. Such identification and validation of the adaptive capacity of population(s) will be crucial for the development of future sustainable management programs.

Lastly, one of the contributions is pioneering an approach that goes beyond SNPs, by extending the genomic variant catalogue to copy number variants (CNVs) as well as transposons and retrotransposons. Cayuela et al. (2022) use an extensive mark–recapture dataset of ~20,000 Columbian spotted frogs *Rana luteiventris* to investigate climate-driven genomic adaptations. Frog populations were studied for 14–18 years along a temperature gradient in the western United States, and several life-history traits, including adult survival, life span, senescence rate, recruitment and population growth, were analysed to detect clinal shifts. This large dataset was then combined with a genome-wide dataset of SNPs, CNVs and transposons to uncover the molecular mechanisms associated with clinal shifts in these life-history traits. Their analysis showed that temperature was the main climatic predictor that influenced life-history evolution in this frog species, notably an acceleration in senescence with increasing temperature. Candidate genes associated with thermal adaptation and a signature of recently diverged transposon and retrotransposon accumulation following temperature stress were uncovered.

4 | FUTURE OUTLOOK: INTEGRATING MULTIPLE GENOMIC AND ENVIRONMENTAL APPROACHES

As the contributions in this Special Feature make clear, genomic approaches and data are beginning to shed light on how species respond to climate change through range shifts, phenotypic plasticity and evolutionary adaptation. Studying patterns of genetic variation from genome-wide SNPs and their association with environmental variables and phenotypes, under both natural as well as controlled laboratory conditions, has been a powerful tool to understand how populations have responded to recent increases in temperature and to predict their future dynamics. However, as Layton and Bradbury (2021) explain in this Special Feature, the genetic basis of such responses encompasses a wide variety of types of genomic variation and thus future studies will need to take a multi-omic approach, beyond only SNPs. For example, structural variants are known to play a role in adaptation and are likely to inform predictions of future climate change responses. Chromosomal inversions can play a role in adaptation by maintaining locally beneficial haplotypes (Fuller et al., 2017; Wellenreuther et al., 2019; Wellenreuther & Bernatchez, 2018), simple sequence repeats have been shown to regulate gene expression (Yuan et al., 2021) and CNVs (e.g. Cayuela et al., 2022) have been used to understand climate-related genotype–phenotype associations. Moreover, the role of epigenetic variation is becoming increasingly recognised as an important component of population and evolutionary responses to climate change (McGuigan et al., 2021). Therefore, Layton and Bradbury argue that structural and epigenetic variation should be incorporated into estimates of climate change vulnerability and can provide additional power for predicting responses, particularly for weakly structured or panmictic species.

In addition to applying multi-omic approaches, more careful experimental design can further improve the strength of causal inference in estimating climate responses. In this Special Feature, Oomen and Hutchings (2022) provide guidance for future studies on how to combine physiological experiments with spatial genetic data to better disentangle causal variation in local adaptation and plasticity across environmental gradients and different spatial scales, and across populations with different demographic histories. Similarly in this Special Feature, Gervais et al. (2022) highlight the importance of addressing potentially confounding issues of biased sampling and insufficiently understood mechanisms in developing inference of climate change response. Specifically, Gervais et al. highlight that animal responses to environmental change often involve behavioural mechanisms, such as dispersal or habitat selection and that these can also be involved in range shift responses. Where such behavioural response mechanisms are themselves heritable, they can lead to positive correlations of genotypes and environments that inflate the apparent environmental influence on performance-related traits, such as thermal tolerance. The role of movement behaviours to inflate performance genotype–environment correlations can thus bias our

predictions of the adaptability of such performance traits to future environmental change. As in Oomen et al., Gervais et al. recommend addressing this problem by combining wild sampling with common garden experiments, and to develop genomic sampling designs on wild populations that explicitly consider and control for differences in movement behaviours among individuals.

5 | CONCLUSIONS

The rapid increase of global temperature presents a significant risk for ecosystems and species world-wide. This threat of climate change is only expected to rise in the coming decades. As highlighted by the contributions in this Special Feature, the emergence of genomic approaches provides a powerful tool to understand and predict how animal species respond to changing environments. These studies demonstrate how multi-omic approaches embedded in a solid ecological framework can be used to reveal the basis of a species response to a warming climate through range shifts, phenotypic plasticity and evolutionary adaptation. Moreover, these contributions show how integrating genomic and environmental data collected across multiple sources, and combined with targeted experiments, can be used to understand and predict future population-level responses.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

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