

Introduction



Cite this article: Fox RJ, Donelson JM, Schunter C, Ravasi T, Gaitán-Espitia JD. 2019 Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Phil. Trans. R. Soc. B* **374**: 20180174. <http://dx.doi.org/10.1098/rstb.2018.0174>

Accepted: 7 December 2018

One contribution of 13 to a theme issue 'The role of plasticity in phenotypic adaptation to rapid environmental change'.

Subject Areas:

ecology, evolution

Keywords:

acclimation, climate change, ecological and evolutionary dynamics, genotype \times environment (G \times E), genetic assimilation, selection

Author for correspondence:

Rebecca J. Fox
e-mail: rebecca.fox@anu.edu.au

Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change

Rebecca J. Fox¹, Jennifer M. Donelson², Celia Schunter³, Timothy Ravasi⁴ and Juan D. Gaitán-Espitia³

¹Division of Ecology and Evolution, Australian National University, Canberra, Australian Capital Territory 2601, Australia

²ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4810, Australia

³The Swire Institute of Marine Science, School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong, SAR, People's Republic of China

⁴KAUST Environmental Epigenetic Program (KEEP), Division of Biological and Environmental Sciences and Engineering, King Abdullah University of Science and Technology, Thuwal 23955-6900, Kingdom of Saudi Arabia

RJF, 0000-0003-3442-4189; JMD, 0000-0002-0039-5300

How populations and species respond to modified environmental conditions is critical to their persistence both now and into the future, particularly given the increasing pace of environmental change. The process of adaptation to novel environmental conditions can occur via two mechanisms: (1) the expression of phenotypic plasticity (the ability of one genotype to express varying phenotypes when exposed to different environmental conditions), and (2) evolution via selection for particular phenotypes, resulting in the modification of genetic variation in the population. Plasticity, because it acts at the level of the individual, is often hailed as a rapid-response mechanism that will enable organisms to adapt and survive in our rapidly changing world. But plasticity can also retard adaptation by shifting the distribution of phenotypes in the population, shielding it from natural selection. In addition to which, not all plastic responses are adaptive—now well-documented in cases of ecological traps. In this theme issue, we aim to present a considered view of plasticity and the role it could play in facilitating or hindering adaptation to environmental change. This introduction provides a re-examination of our current understanding of the role of phenotypic plasticity in adaptation and sets the theme issue's contributions in their broader context. Four key themes emerge: the need to measure plasticity across both space and time; the importance of the past in predicting the future; the importance of the link between plasticity and sexual selection; and the need to understand more about the nature of selection on plasticity itself. We conclude by advocating the need for cross-disciplinary collaborations to settle the question of whether plasticity will promote or retard species' rates of adaptation to ever-more stressful environmental conditions.

This article is part of the theme issue 'The role of plasticity in phenotypic adaptation to rapid environmental change'.

1. Introduction

'The love of complexity without reductionism makes art; the love of complexity with reductionism makes science'

E.O. Wilson [1]

Phenotypic plasticity is the ability of an individual genotype to produce different phenotypes in response to the environment. Since plasticity is a property of the individual, it is often hailed as a rapid-response mechanism that will enable organisms to adapt and survive in our rapidly changing world (sometimes termed 'plastic rescue') [2–4]. But plasticity can also retard adaptation by shifting the distribution of phenotypes in the population closer to the optimum, thus shielding genes from natural selection [5]. In addition, plasticity can be

maladaptive, meaning that it does not always facilitate selection for adaptive genotypes [6,7]. Our theme issue aims to bring together these tensions that surround the precise nature of plasticity and to provide a re-examination of the role of plasticity in phenotypic adaptation to rapid environmental change.

The scope of this theme issue, and by extension the research interests it encompasses, are broad. This is partially reflected in the diverse fields of our editorial group and of contributors to this theme issue (ecology, quantitative-genetics, biomedical science, experimental evolutionary biology, epigenetics, genomics and molecular biology). Yet we have all ended up struggling to answer the same kinds of questions. How will the performance of populations and species respond to environmental change? What is the respective contribution of evolution and plasticity in determining rates of adaptation or in facilitating species' persistence? Meanwhile, the contextual landscape of the research agenda is shifting. A debate between those who consider 'plasticity-first' to promote adaptation and those for whom adaptive responses occur via genetic changes alone, with plasticity buffering those genetic responses, simmers on [8–12]. However, we operate now in a time when it is hard to find a study that rejects plasticity as a potential source of adaptation to novel environments. To our mind, the debate now centres on the distinction between when plasticity is an adaptation (itself the result of evolution via natural selection), or simply yields an adaptive outcome (i.e. fortuitously increases fitness) [7,13]. Our aim for this theme issue is not to dwell on distinctions or discord but to help integrate different perspectives and focus attention on common ground: to highlight the growing consensus view of plasticity and adaptive evolution [14].

There is almost universal acknowledgement that plasticity has an important role to play in species' adaptation to human-induced environmental change [4,14]. As Merilä & Hendry [7] point out, it could be argued that the pendulum has now swung so far that plasticity is treated as the null model for phenotypic change under environmental variation and rejected only if direct evidence of genetic change is recorded. It is important to step back and re-examine our current understanding of the role of phenotypic plasticity *relative* to adaptive evolution in promoting adaptation to novel environments. We highlight here the fact that different types of plasticity act on very different timescales and are not all of equal importance when it comes to adaptation to rapid environmental change. Understanding the mechanisms regulating plasticity will be important in determining whether a particular response is adaptive (highlighted by Snell-Rood *et al.* [4]) and many of the contributions to this theme issue reiterate this point. For example, behavioural plasticity is typically assumed to be a low-cost, rapid response. But, depending on the underlying mechanism, behavioural plasticity is either activational (high-cost, but quick response) or developmental (lower-cost but slower-acting and with more integrated response outcomes) [15]. Similarly, transgenerational plasticity (TGP) is likely to operate on a slower timescale that puts it more on a par with adaptive evolution [16–18]. The type and mechanism of plasticity involved will therefore affect the costs incurred by the individual and determine whether the plasticity is likely to be adaptive on a timescale relevant to the pace of environmental change. In their recent review, Snell-Rood *et al.* [4] argue that highly adaptive plasticity is likely to be the most costly and slow-acting form, resulting in less pronounced evolutionary responses at the overall

population level. Accordingly, plasticity may buy time for populations, but whether it will be enough, given the rate of environmental change, is unknown. We cannot assume that plasticity, just because it acts at the level of the individual, is a faster-acting mechanism of adaptation than evolution arising through differential survival of genotypes. Depending on the nature and speed of the environmental change, either evolutionary rescue, plastic rescue or a combination of the two may bring about population recovery and persistence. This theme issue does not pretend to encompass all the current research approaches, nor the wealth of research knowledge that already exists in the studies of phenotypic plasticity, G × E interactions and rates of population fitness evolution via natural selection. Instead, our aim is to concentrate on the interplay between adaptive evolution and plasticity, placing them *together* in the context of environmental change.

The contributions to this theme issue fit into four broad themes. First, the multidimensional nature of the challenge of determining the role of plasticity in adaptation to novel environments. This theme issue highlights the fact that the study of plasticity and its potential to be adaptive needs to be inclusive of time *and* space. Our second theme is the role of the past in predicting the future. Here we highlight the fact that predicting levels of expression of phenotypic plasticity within a population into the future requires an understanding of the influence of past environmental changes on current levels of plasticity. Our third theme centres on the role of sexual selection and mate choice as an understudied, yet crucial, aspect of determining the role of phenotypic plasticity in adaptation to novel environments. Finally, by taking a somewhat reductionist view of plasticity as equivalent to condition-dependence, the fourth theme of the issue emerges: that of plasticity as a 'Matthew effect'—initial advantages lead to further cumulative advantages. This provides a context in which one can start to understand why inter-individual patterns are predictable.

2. The space–time continuum: plasticity across multiple dimensions

'Nothing remains the same from one moment to the next, you can't step in the same river twice' (Ursula K. Le Guin [19])

The need to understand plasticity through time in relation to rapid environmental change is evidenced by the number of papers within this theme issue that explore cross-generational exposure, using a range of focal species [20–23]. These studies highlight key questions and challenges in relation to identifying phenotypic adaptation. One such question is whether transgenerational transmission depends on parent-of-origin, which is important to understand in relation to mechanisms and adaptive potential. In Emborski & Mikheyev's study [21] on fruit flies (*Drosophila melanogaster*), some phenotypic traits (triglyceride level) showed parent-of-origin effects, while others (sugar level) did not. In addition, both Fuxjäger *et al.* [20] and Emborski & Mikheyev [21] demonstrate that phenotypic changes can be sex-specific. When the focus is at the individual level, trade-offs between traits can occur, which could reduce adaptive potential with transgenerational exposure, as seen in the polychaete (*Ophryotrocha labronica*) [23]. Furthermore, these studies find evidence that trade-offs can be amplified when there are multiple stressors, which is likely to be a common scenario for most species in the future.

Another important aspect of phenotypic adaptation is the interplay between within- and transgenerational plasticity and how environmental conditions experienced by the previous and current generation interact. In this theme issue both Fuxjäger *et al.* [20] and Baker *et al.* [22] highlight that beneficial (i.e. adaptive) TGP can be context-dependent. In sticklebacks (*Gasterosteus aculeatus*), parental exposure to elevated water temperature was beneficial for mating success, but only when offspring also developed in the elevated thermal conditions [20]. For the annual plant, the redshank (*Polygonum persicaria*), parental shade increased the reproductive output of progeny in neighbour and understory shade conditions but decreased that of progeny in sunny dry conditions [22]. In cases such as these, TGP could be adaptive if environmental conditions are changing directionally but maladaptive if environmental conditions vary erratically either through time (greater environmental variation is a future projection for many ecosystems) or space (i.e. between patches or across a species range).

One key factor to emphasize is ‘environmental condition’, as the plastic response within-generations and across-generations depends on environmental cues that are used to make behavioural and life-history choices [24]. However, when these cues are altered, for instance, by anthropogenic change, their reliability may be diminished. Well-documented examples include the impact of polarized light pollution on insect species that typically use water reflection as a cue for suitable breeding sites, but can be tricked into laying on artificial polarizing surfaces. This change towards a lower-quality environment, triggered by a decline in the reliability of the cue, has been labelled an ‘ecological trap’ [25]. In this theme issue, Bonamour *et al.* [26] highlight the need to evaluate the reliability of environmental cues to understand how adaptive plastic responses might be. Their review and case study on avian phenology provides a helpful guide for researchers attempting to understand the effects of global change at the ecological level.

Of course, from a conservation perspective, projecting species’ responses to environmental change requires a wider understanding: not just the response of a single population, but of the numerous populations that make up a species. The responses and persistence of species in the face of environmental change relate to the *combination* of phenotypic plasticity, genetic diversity and selection and their interaction with ecological processes of dispersal and migration across a species’ range. These aspects are rarely considered holistically and for most species, an understanding of their interplay is not available. In distribution modelling of species, however, the importance of factors such as local adaptation and plasticity can be clearly observed as their inclusion results in dramatic shifts in predicted ranges [27–31]. In this theme issue, Donelson *et al.* [32] discuss how, for marine species, ecological and evolutionary processes (migration, plasticity, selection) in response to ocean warming are likely to play out differently depending on the location within a species’ range. They describe a conceptual model and outline general expectations for adaptive processes operating in a species’ range, as well as evidence currently available in support of those expectations. They discuss potential applications of their model to project community-level responses of marine organisms to environmental change and highlight the challenges that still exist for empiricists to collect relevant data that will allow for the incorporation of plastic and adaptive process into projections of population responses to climate change.

3. Genetic accommodation, assimilation and the role of the past in predicting the future

‘The past is never dead. It’s not even past’

(W. Faulkner, *Requiem for a Nun* [33])

The ability of species to respond to future environmental change will not be independent of previous environmental experience. Historical conditions impose selection, resulting in the adaptation of populations to the range, average, extreme and/or variation in conditions experienced. Owing to the costs associated with sensing and responding to environmental change via phenotypic plasticity [34], it is often thought that species that have not experienced environmental fluctuations will have limited capacity to respond phenotypically to future change. On a broad scale, there is good empirical evidence to support this, with plasticity varying depending on the level of environmental heterogeneity within and between patches/populations [35,36]. Genetic variation is known to be an important predictor of plastic and adaptive potential. For example, reduced genetic variation owing to strong positive selection or limitations on recruitment or migration can reduce the capacity for phenotypic plasticity [2,37,38]. Alternatively, traits that were once plastic can become fixed or expressed constitutively in the population (i.e. genetic assimilation [39]). The existence and prevalence of genetic assimilation are still controversial, but it has the potential to play an influential role in how species respond to rapid environmental change.

The importance and magnitude of the interaction between genetic variation and phenotypic plasticity in spatially adapted populations is still unclear. Here, Kelly [40] tackles the thorny issue of how we can advance our understanding of whether populations will persist via plasticity or adaptation, or a combination of the two. She suggests several useful proxies (space-for-time substitutions, estimates of genomic divergence at environmentally responsive gene loci) that could be used as ways of determining the relative contributions of the two in responses to climate change. The evidence presented in Kelly’s review suggests that evolutionary changes play a significant role in adaptation to climate change, but it is still uncertain as to whether that role is more or less important than the contribution of evolving plasticity—or even whether evolving plasticity more often facilitates or retards evolutionary rescue. In terms of the latter conundrum, her prescription is twofold: (1) more experimental evolution studies that test whether greater genetic variation for plasticity in a population increases the probability of persistence (i.e. plastic rescue) and (2) comparative studies using invasive species to test whether more successful invaders have greater genetic variation for plasticity. If taken up, the prescription would facilitate our understanding of the potential for populations or species to adapt to environmental change via the route of plasticity followed by assimilation of plastic phenotypes and allow us to make predictions regarding population persistence based on our understanding of past changes in plasticity: using the past to predict the future.

Of course, the environment also has a past, one through which the phenotypic and genetic variation we observe today in natural populations has arisen and been maintained. However, the variation we observe at this particular point in time may not be the full story, and the past may provide some additional clues. Salinas *et al.* [41] investigate the effect of extreme thermal environments on cryptic variation and phenotypic plasticity. This so-called ‘hidden’ variation is a

critical component of the adaptive capacity of populations because, under novel conditions, it generates heritable phenotypic variation [42]. Increased trait variation can lead to significant ecological and evolutionary changes. Although some empirical support for this claim exists, it is also well established that physiological mechanisms change when organisms are exposed to constant versus fluctuating temperatures. Salinas *et al.* [41] test this idea by analysing the effects of novel extreme temperatures and thermal variation on life-history and morphological traits of fathead minnow, *Pimephales promelas*. Their results are consistent with the temperature–size rule; mean values of the traits decreased as temperatures increased. This was evident for both constant and fluctuating conditions. However, the overall variance in length-at-age and CT_{max} was lower under the more stressful conditions of fluctuating temperatures than when temperatures were constant, which is suggestive of strong genetic correlations between stressful and benign environments. As Salinas *et al.* [41] point out, this means that the shape of the reaction norm under past conditions can be an important predictor of trait values under environmental stress, highlighting again the importance of the past in predicting the future.

4. It matters who you mate with: the importance of sex

'What is the meaning of life? ... I'm afraid the answer is disappointingly simple: Mating. That's it'.

(Oliver Markus [43])

The third theme of our special theme issue tackles the topic of sexual selection and its relationship with plasticity and adaptation to novel environments. As Fox *et al.* [44] point out, the effects of plasticity on adaptation to novel environments matter little if individuals that exhibit plasticity do not mate more often than those that do not. The process of adaptation requires an increase in mean population fitness over time. Since sexual selection (a selection that arises from differential mating success among competing individuals) often results in 'healthier' males having higher mating success, it should result in accelerated 'purging' of mutations from the genome [45,46], and an associated increase in female fitness through time [47,48]. Sexual selection should therefore promote adaptation to novel environments if there is a positive genetic correlation between male sexual traits and female fitness, *and* if additive genetic variance persists under conditions of stress in the novel environment, *and* if these advantageous male traits are still reliable indicators of female fitness in the novel environment [49]. Despite the appeal of the argument that sexual selection is beneficial, both experimental evidence (reviewed in [50,51]) and theoretical models [52] are equivocal. We therefore still know relatively little about how sexual selection will affect species' response to global change. Adding phenotypic plasticity into the mix means having to consider further how the plastic expression of sexual traits affects the strength and direction of sexual selection in novel environments. Beyond that, we can also ask how sexual selection, occurring predominantly as male–male competition, female mate-choice and sperm competition, might itself favour the evolution of plasticity by selecting for males with greater plasticity.

However, as others have previously noted, there are several sticking points in the claim that sexual selection promotes

adaptation. First, do condition-dependent male sexual traits actually elevate female reproductive output [50,53]? Second, is sexual selection in males always stronger than in females? (In other words, does sexual selection really purge deleterious alleles at a faster rate than natural selection?) [54]. Third, can additive genetic variance be maintained under sexual selection when the environment is changing rapidly [55]? Finally, is intra-locus sexual conflict (owing to sexually antagonistic genes that increase male mating success but lower female reproductive output) reduced under novel environmental conditions [56,57]? The evidence remains equivocal, so we are still unable to state whether sexual selection promotes or retards adaptation under environmental change. There is even less certainty when we add plasticity to the mix. If one considers the role of female reproductive output in determining population extinction risk under global change, it is surprising that so few studies address the combined effects of plasticity and sexual selection on rates of adaptation.

In this theme issue, Fox *et al.* [44] review the existing literature, noting that asking how plasticity in sexually selected traits affects adaptation to rapid environmental change can be pragmatically reduced to asking if condition-dependent and socially dependent expression of male traits elevates female lifetime reproductive success. The other two contributions in this section tackle aspects of this question from an empirical perspective. Kelly *et al.* [58] ask whether females preferentially choose males who sire more plastic offspring. They find that, in spadefoot toads, male call rates (a signal used by females to choose mates) not only predict the degree of morphological plasticity of the offspring they sire, but that offspring with higher morphological plasticity have higher fitness. The male sexual signals may therefore be honest signals of adaptive plasticity, so sexual selection *favours* the evolution of plasticity. Assuming that plasticity is adaptive in the particular environmental context, sexual selection could then enhance the rate of adaptation to local environmental conditions [58]. Fuxjäger *et al.* [20] delve further into the idea that the transmission of plasticity across generations can elevate the reproductive success of offspring. For the oceanic stickleback, paternal thermal history had a significant effect on a son's mating success under stressful environmental conditions. In elevated temperature conditions, the sons of male sticklebacks reared at the same temperature as their fathers were more successful at attracting females to breed than sons whose fathers had been raised at lower water temperatures. This suggests that cross-generational plasticity might play a role in elevating the reproductive success of sons. At the elevated water temperature, females chose to breed with smaller males regardless of their own size, suggestive of adaptive plasticity in female mate-choice under altered environmental conditions. However, as Fox *et al.* [44] point out, the key to population survival under environmental change is the reproductive success of daughters. In the study by Fuxjäger *et al.* [20], female mating success and clutch size were significantly lower at elevated temperatures, but the daughters of parents reared at the higher temperatures were not negatively impacted, suggesting that TGP of male body size could elevate the reproductive success of their daughters.

5. Plasticity as a 'Matthew effect'

'The rich get richer and the poor get poorer' (Percy Bysshe Shelley, *A defence of poetry* [59])

The term 'Matthew effect' refers to the theory that initial advantages lead to further cumulative advantages. The term has been adopted in multiple fields (see [60]), including perhaps most famously in education where it is used to encapsulate the idea that early acquisition of reading skills gives an advantage to the bearer once learning becomes dependent on reading ability and the gap in learning outcomes between the 'fast' and 'slow' readers becomes accentuated [61]. The condition-dependence of plasticity could, arguably, be viewed in the same way as setting up a 'Matthew effect' in individual rates of adaptation, whereby high-condition individuals have the opportunity to show adaptive, plastic responses to rapid environmental change and low-condition individuals fall by the wayside. The condition-dependent nature of plasticity is a fundamental but often disregarded aspect to be borne in mind when considering the effect of environmental change on population persistence. It means that plasticity essentially functions as an amplifier for traits that already show condition-dependence (as is the case for many sexually selected traits (see [44])), increasing the strength of the signal.

The physiological 'tool-kit' that individuals have at their disposal (e.g. metabolic adjustments) in order to generate rapid plastic responses will necessarily have been shaped by evolutionary history. Physiological traits, although acting in the short-term, therefore have a basis in longer-term, evolutionary timescales [62,63], meaning that initial advantages could lead to further cumulative advantages. In animals, metabolic adjustments involve changes in the rates of energy uptake and allocation (i.e. metabolic rates) among competing functions at the whole-organism level (i.e. maintenance, reproduction, growth, storage), which are conditioned by the capacity of mitochondria to provide sufficient aerobic energy at the cellular level (ATP) [64]. Here, Norin & Metcalfe [65] explore this theoretical framework with the aim of clarifying our understanding of the physiological/cellular mechanisms underlying plasticity of metabolic rates, the associated cost/benefits of metabolic plasticity, and the potential evolutionary responses of these traits to environmental change. As with many other physiological traits, metabolic rates can be highly plastic in response to changes in either the animal's internal state or its environment. However, the degree of phenotypic plasticity differs among components of the metabolic budget (i.e. metabolic ceiling and floor) owing to energetic constraints and differences in energy demands of tissues and organs. Moreover, the plasticity of metabolic rates can vary across time within individuals (i.e. owing to seasonal changes), as well as among individuals (i.e. intra-population differences in energy demands) and populations (i.e. owing to local adaptation), all of which suggests that phenotypic plasticity of metabolic rate is context-dependent and promotes the resilience of organisms and populations to environmental changes, with short-term benefits in terms of energy savings during stressful conditions. However, plastic metabolic rates also have associated costs and limitations in terms of trade-offs that result from changes in energy allocation among organismal functions. The balance between costs and benefits of having flexible metabolic rates and the amount of additive genetic variation in these traits will ultimately determine the capacity of organisms and populations to cope with and adapt in changing environments.

The phenotypic plasticity of individual traits can vary across geographical scales depending on the particular

environmental (i.e. local climate) and genetic contexts of natural populations (e.g. [66]). In principle, this geographical variation in phenotypic plasticity has the potential to create gradients of selection across the species' distribution, influencing the evolutionary dynamics of populations [67] and their adaptive capacity in changing environments (e.g. [68]). However, despite these assumptions, we are still far from understanding the extent to which phenotypic plasticity constitutes an adaptive response to changing environmental conditions, and hence the nature of selection on plasticity itself [69]. In this theme issue, Arnold *et al.* [70] address this major gap in our knowledge by conducting a review and meta-analysis of selection on thermal phenotypic plasticity. Considering the large body of literature documenting thermal plasticity, it is surprising that only very few studies have estimated coefficients of selection on measures of plasticity. These studies do not provide strong support for selection on plasticity, with the majority of estimates of directional selection on plasticity being weak and non-significant, and no evidence for selection on plasticity overall. Perhaps, then, initial advantages of plasticity do *not* lead to further cumulative advantages, and plasticity itself is not subject to a Matthew effect? More studies are needed before we can generalize their findings at a broader scale, but the analysis of selection on plasticity is still challenging and a major constraint. In order to deal with these issues, Arnold *et al.* [70] propose a promising statistical approach based on multivariate mixed models to estimate plasticity (as reaction norm slope) and selection on plasticity jointly in a single step of the analysis, thus avoiding the problems of having to do 'statistics-on-statistics'.

As both the strength and shape of selection are key elements that impact the speed at which populations can evolve, determining whether selection in nature targets plasticity itself is of paramount importance. This is particularly relevant if we want to understand how organisms respond to fluctuating environments and whether they will be able to adapt in the face of climate change [71].

6. Conclusion

How species and populations can respond to modified environmental conditions is critical to their persistence both now and especially with the ever-increasing pace of environmental change. There is no doubt that the capacity of individuals to display phenotypic plasticity, as well as the capacity for adaptation to occur at the population level, will determine the winners and losers under future anthropogenic environmental change. A significant amount of research effort is currently dedicated to understanding and predicting likely biological responses to climate change, yet processes of plasticity and adaptation are often considered independent of each other. However the two should be viewed synergistically, because they are not independent. In compiling the articles for this theme issue, our aim has been to present a balanced assessment of plasticity and the role it could play in either aiding or hindering species' adaption to rapid environmental change. To do so, we have brought together contributors from across biological disciplines, all of whom come with different perspectives on the relative roles of plasticity and evolution in determining species' ability to persist and adapt to novel environments. The study

systems of our contributors are equally broad, covering plants, invertebrates, amphibians, birds and marine and freshwater fishes.

There are many topics that, for practical reasons of space, we have not been able to address in this theme issue, including the molecular mechanisms underpinning plasticity—an important field that could potentially be the subject of its own special issue. After all, the genome and, more especially, its regulation must be highly dynamic to allow for plasticity to occur and we need to learn more about both genetic and epigenetic mechanisms to understand how climate stressors can influence and shape genomes, transcriptomes and the epigenome, in particular, across generations. In recent years, considerable effort has been expended on trying to understand the molecular, genomic and epigenomic mechanisms underlying responses to climate stressors across a variety of species and populations, including fish [72–76], corals [77,78], other invertebrates [79–81] and plants (review: [82]). In the process, we have substantially increased our knowledge of the molecular mechanisms underlying plasticity (e.g. [72]), as well as the interplay between genetic variation and TGP [40,73], and the importance of the role of local adaptation [83].

Although much work has already been done to uncover the molecular processes underpinning plasticity, we are just scratching the surface and many questions remain. The ultimate goal is an understanding of how plasticity and genetic variation influence each other and, as a consequence, the extinction risk of a population under environmental stress. To reach this goal will require knowledge of, among other things, the extent of the parental contribution to offspring plasticity and the full suite of epigenetic mechanisms controlling plasticity. Recent moves towards the establishment of more interdisciplinary teams from across the various strands of biology represent an important acknowledgement that no one strand has the answer. Insights from evolutionary biology, ecology, physiology and molecular biology are required. Success will come from a combination of field-based ecological studies, long-term life-history datasets, laboratory-based experimental evolution and the latest advances in genomics [84]. In almost every discussion that we have had with theoreticians and empiricists regarding the link between plasticity and adaptive evolution, we inevitably end up back at the ‘big questions’. To what extent is plasticity adaptive? What are the costs and limitations of plasticity? What environmental and organismal characteristics favour the evolution of plasticity (cf. [85])? The fact that we are still grappling with the fundamentals of the

problem impacts on our ability to come up with real-world, prescriptive solutions to the applied conservation and ecosystem management challenges that are already being posed by rapid environmental change. But this is not a cause for despair. Instead, our interpretation is more positive: there is still so much left to answer, and we, as scientists, must rise to the challenge. It is our job to find solutions and an interdisciplinary approach appears to be the best way forward.

It is often said that we have moved beyond the consideration of plasticity as a ‘nuisance’ to an acceptance of its fundamental role in an organism’s response to changing environmental conditions [86]. While we agree that the study of plasticity, or GxE, is now well-and-truly at the forefront of evolutionary and ecological studies, we suggest that until there exists a more complete understanding of plastic responses under heterogeneous environments (based on empirical experimentation) and a theoretical framework for predicting the optimal multi-trait response to condition-dependence, the question of whether plasticity will be adaptive under future environmental change remains something of a ‘nuisance’. We cannot ignore it, however, so let us put our collective expertise and wisdom to the task of determining the role of plasticity in phenotypic adaptation to rapid environmental change. The 12 articles in this theme issue represent the latest ideas and approaches by researchers from a range of disciplines, backgrounds and study systems. Our hope is that by bringing these different approaches under one roof, we can inspire cross-fertilization of ideas and sow the seeds of new collaborations.

Data accessibility. This article has no supporting data.

Competing interests. We declare we have no competing interests

Funding. The authors were supported by the Australian Research Council (J.M.D. and R.J.F.), The University of Hong Kong (J.D.G.-E. and C.S.) and King Abdullah University of Science and Technology (T.R., C.S. and J.M.D.)

Acknowledgements. We thank the Editorial Board of *Philosophical Transactions of the Royal Society* for giving a team comprised largely of early- and mid-career researchers the opportunity to put this theme issue together. We thank all of our wonderful contributors for agreeing to work with us and for their cooperation throughout the submission process. We also thank the 13 women and 14 men who generously gave up their valuable time to peer-review the theme issue contributions, as well as Phil Munday and Mike Jennions for helpful comments on an earlier version of this Introduction. Thank you to the incredible artist Damien Veal for collaborating with us, *pro bono*, to create the cover image for the theme issue. Finally, we particularly thank Helen Eaton, Senior Commissioning Editor, for all her incredible support and help during the process of bringing this theme issue to fruition.



Jennifer Donelson is currently a Postdoctoral Research Fellow at the ARC Centre of Excellence for Coral Reef Studies located at James Cook University in Townsville Australia. Her love for the ocean led her to complete her PhD in 2012 at James Cook University, before becoming a Chancellor’s Postdoctoral Fellow in the School of Life Sciences at the University of Technology, Sydney from 2013–2016. Jenni’s research began with an interest in parental effects and the impact that environmental quality has on offspring phenotypes, subsequently expanding to explore the capacity for within- and across-generational plasticity to ocean warming in marine fish. Her current research continues to focus on the plastic and adaptive capacity of marine fish in the face of changing environmental conditions.



Juan Diego Gaitán Espitia is an evolutionary ecologist from Colombia, currently working as Assistant Professor at the School of Biological Sciences and Swire Institute of Marine Science—University of Hong Kong. He is the PI of the iBEER Lab (Integrative Biology and Evolutionary Ecology Research group) working on eco-evolutionary dynamics, mechanisms of local adaptation and phenotypic/genetic divergence. He received his BSc and MSc in Marine Biology from the Jorge Tadeo Lozano University (Colombia) and his PhD in Ecology and Evolution from the Austral University of Chile. Juan is particularly interested in the understanding of adaptive evolution of physiological and life-history traits along environmental gradients and in response to anthropogenic changes.



Rebecca Fox is currently a Postdoctoral Research Fellow in the Division of Ecology and Evolution at The Australian National University, Canberra. She received her PhD in Marine Biology from James Cook University, Australia in 2013, followed by a Chancellor's Postdoctoral Fellowship in the School of Life Sciences at the University of Technology Sydney. She holds a BA(Hons) in Philosophy, Politics and Economics (P.P.E) from the University of Oxford and a Masters in Economics from McGill University, Canada. Rebecca now combines her twin interests of ecology and economics within an evolutionary context, studying facets of sexual selection such as condition-dependence of resource allocation across sexual traits.



Celia Schunter, coming from a land-locked place, was always fascinated by the marine world. Early in her career, she started combining the study of marine organisms with genetic and molecular tools. She received her BSc in Marine Biology from James Cook University, Australia and her Masters and PhD in Genetics from the University of Barcelona, Spain. During her Postdoc at the King Abdullah University of Science and Technology in Saudi Arabia, she used functional genomics to understand the effects of ocean acidification on fish within and across generations. Currently, she is an Assistant Professor at the Swire Institute of Marine Sciences at the University of Hong Kong, where her laboratory continues to explore impacts of climate change on behaviour and population dynamics of marine organisms, including the underlying molecular mechanisms of adaptation.



Timothy Ravasi is a Professor of Marine Genomics, an Adjunct Professor at the University of California, San Diego and a Visiting Scientist at the RIKEN Institute in Japan. Coming from Italy, he grew up on the shores of the Madrilanian Sea. After receiving his doctoral degree from the University of Milan, he started his postdoctoral training at the Institute for Molecular Biosciences at the University of Queensland in Australia. He then moved to the University of California, San Diego. In 2008, he joined the faculty of the newly founded King Abdullah University of Science and Technology (KAUST) in Saudi Arabia, where in 2014 he was promoted to full Professor. At KAUST, Prof. Ravasi established a multi-disciplinary research program aiming to understand the effects of climate change on coral reef ecosystems, in particular on fish communities.

References

1. Wilson EO. 1999 *Consilience: the unity of knowledge*. London, UK: Abacus.
2. Chevin L-M, Lande R, Mace GM. 2010 Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* **8**, e1000357. (doi:10.1371/journal.pbio.1000357)
3. Chevin L-M, Lande R. 2010 When do adaptive plasticity and genetic evolution prevent extinction of a density regulated population? *Evolution* **64**, 1143–1150. (doi:10.1111/j.1558-5646.2009.00875.x)
4. Snell-Rood EC, Kobiela ME, Sikkink KL, Shepherd AM. 2018 Mechanisms of plastic rescue in novel environments. *Ann. Rev. Ecol. Evol. Syst.* **49**, 331–354. (doi:10.1146/annurev-ecolsys-110617-062622)
5. Huey RB, Hertz P, Sinervo B. 2003 Behavioural drive versus behavioural inertia in evolution: a null model approach. *Am. Nat.* **161**, 357–366. (doi:10.1086/346135)
6. Ghalambor CK, McKay JK, Carroll SP, Reznick DN. 2007 Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* **21**, 394–407. (doi:10.1111/j.1365-2435.2007.01283.x)

7. Merilä J, Hendry AP. 2013 Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol. Appl.* **7**, 1–14. (doi:10.1111/eva.12137)
8. Crispo E. 2007 The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution* **61**, 2469–2479. (doi:10.1111/j.1558-5646.2007.00203.x)
9. Moczek AP. 2007 Developmental capacitance, genetic accommodation, and adaptive evolution. *Evol. Dev.* **9**, 299–305 (doi:10.1111/j.1525-142X.2007.00162.x)
10. Badyaev AV. 2009 Evolutionary significance of phenotypic accommodation in novel environments: an empirical test of the Baldwin effect. *Phil. Trans. R. Soc. B* **364**, 1125–1141. (doi:10.1098/rstb.2008.0285)
11. Levis NA, Pfennig DW. 2016 Evaluating ‘plasticity-first’ evolution in nature: key criteria and empirical approaches. *Trends Ecol. Evol.* **31**, 563–574. (doi:10.1016/j.tree.2016.03.012)
12. Corl A, Bi K, Luke C, Challa AS, Stern AJ, Sinervo B, Nielsen R. 2018 The genetic basis of adaptation following plastic changes in coloration in a novel environment. *Curr. Biol.* **28**, 2970–2977. (doi:10.1016/j.cub.2018.06.075)
13. Gotthard K, Nylin S. 1995 Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* **74**, 3–17. (doi:10.2307/3545669)
14. Hollander J, Snell-Rood E, Foster S. 2015 New frontiers in phenotypic plasticity and evolution. *Heredity* **115**, 273–275. (doi:10.1038/hdy.2015.64)
15. Snell-Rood EC. 2013 An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* **85**, 1004–1011. (doi:10.1016/j.anbehav.2012.12.031)
16. Munday PL, Warner RR, Monro K, Pandolfi JM, Marshall DJ. 2013 Predicting evolutionary responses to climate change in the sea. *Ecol. Lett.* **16**, 1488–1500. (doi:10.1111/ele.12185)
17. Salinas S, Brown SC, Mangel M, Munch SB. 2013 Non-genetic inheritance and changing environments. *Non-Genetic Inheritance* **1**, 38–50. (doi:10.2478/ngi-2013-0005)
18. Donelson JM, Salinas S, Munday PL, Shama LNS. 2018 Transgenerational plasticity and climate change experiments: where do we go from here? *Global Change Biol.* **24**, 13–34. (doi:10.1111/gcb.13903)
19. Le Guin U. 1971 *The lathe of heaven*. New York, NY: Scribner.
20. Fuxjäger L, Wanzenböck S, Ringler E, Wegner KM, Ahnelt H, Shama LNS. 2019 Within-generation and transgenerational plasticity of mate choice in oceanic stickleback under climate change. *Phil. Trans. R. Soc. B* **374**, 20180183. (doi:10.1098/rstb.2018.0183)
21. Emborski C, Mikhayev AS. 2019 Ancestral diet transgenerationally influences offspring in a parent-of-origin and sex-specific manner. *Phil. Trans. R. Soc. B* **374**, 20180181. (doi:10.1098/rstb.2018.0181)
22. Baker BH, Sultan SE, Lopez-Ichikawa M, Waterman R. 2019 Transgenerational effects of parental light environment on progeny competitive performance and lifetime fitness. *Phil. Trans. R. Soc. B* **374**, 20180182. (doi:10.1098/rstb.2018.0182)
23. Jarrold MD, Chakravarti LJ, Gibbin EM, Christen F, Massamba-N’Siala G, Blier PU, Calosi P. 2019 Life-history trade-offs and limitations associated with phenotypic adaptation under future ocean warming and elevated salinity. *Phil. Trans. R. Soc. B* **374**, 20180428. (doi:10.1098/rstb.2018.0428)
24. Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA. 2005 Ecological consequences of phenotypic plasticity. *Trends Ecol. Evol.* **20**, 685–692. (doi:10.1016/j.tree.2005.08.002)
25. Schlaepfer MA, Runge MC, Sherman PW. 2002 Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**, 474–480. (doi:10.1016/S0169-5347(02)02580-6)
26. Bonamour S, Chevin L-M, Charmantier A, Teplitsky C. 2019 Phenotypic plasticity in response to climate change: the importance of cue variation. *Phil. Trans. R. Soc. B* **374**, 20180178. (doi:10.1098/rstb.2018.0178)
27. O’Neill GA, Hamann A, Wang T. 2008 Accounting for population variation improves estimates of the impact of climate change on species’ growth and distribution. *J. Appl. Ecol.* **45**, 1040–1049. (doi:10.1111/j.1365-2664.2008.01472.x)
28. Atkins KE, Travis MJM. 2010 Local adaptation and the evolution of species’ ranges under climate change. *J. Theor. Biol.* **266**, 449–457. (doi:10.1016/j.jtbi.2010.07.014)
29. Wang T, O’Neill GA, Aitken SN. 2010 Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecol. Appl.* **20**, 153–163. (doi:10.1890/08-2257.1)
30. Valladares F *et al.* 2014 The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol. Lett.* **17**, 1351–1364. (doi:10.1111/ele.12348)
31. Cacciapaglia C, van Woesik R. 2018 Marine species distribution modelling and the effects of genetic isolation under climate change. *J. Biogeogr.* **45**, 154–163. (doi:10.1111/jbi.13115)
32. Donelson JM *et al.* 2019 Understanding interactions between plasticity, adaptation and range shifts in response to marine environmental change. *Phil. Trans. R. Soc. B* **374**, 20180186. (doi:10.1098/rstb.2018.0186)
33. Faulkner W. 1951 *Requiem for a nun*. New York, NY: Random House.
34. Angilletta M. 2009 *Thermal adaptation: a theoretical and empirical synthesis*, pp. 302. Oxford, UK: Oxford University Press.
35. Schoepner NM, Relyea RA. 2009 Phenotypic plasticity in response to fine-grained environmental variation in predation. *Funct. Ecol.* **23**, 587–594. (doi:10.1111/j.1365-2435.2008.01525.x)
36. Baythavong BS. 2011 Linking the spatial scale of environmental variation and the evolution of phenotypic plasticity: selection favors adaptive plasticity in fine-grained environments. *Am. Nat.* **178**, 75–87. (doi:10.1086/660281)
37. Snell-Rood EC, van Dyken JD, Cruickshank T, Wade MJ, Moczek AP. 2010 Towards a population genetic framework of developmental evolution: the costs, limits and consequences of phenotypic plasticity. *Bioessays* **32**, 71–81. (doi:10.1002/bies.200900132)
38. Murren CJ *et al.* 2015 Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity* **115**, 293–301. (doi:10.1038/hdy.2015.8)
39. Ehrenreich IM, Pfennig DW. 2016 Genetic assimilation: a review of its potential proximate causes and evolutionary consequences. *Ann. Bot.* **117**, 769–779. (doi:10.1093/aob/mcv130)
40. Kelly M. 2019 Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. *Phil. Trans. R. Soc. B* **374**, 20180176. (doi:10.1098/rstb.2018.0176)
41. Salinas S, Irvine SE, Schertzing CL, Golden SQ, Munch SB. 2019 Trait variation in extreme thermal environments under constant and fluctuating temperatures. *Phil. Trans. R. Soc. B* **374**, 20180177. (doi:10.1098/rstb.2018.0177)
42. Paaby AB, Rockman MV. 2014 Cryptic genetic variation: evolution’s hidden substrate. *Nat. Rev. Genetics* **15**, 247. (doi:10.1038/nrg3688)
43. Malloy OM. 2017 *Why men and women can’t be friends*. Los Angeles, CA: Becker & Mally LLC.
44. Fox RJ, Fromhage L, Jennions MD. 2019 Sexual selection, phenotypic plasticity and female reproductive output. *Phil. Trans. R. Soc. B* **374**, 20180184. (doi:10.1098/rstb.2018.0184)
45. Whitlock MC, Agrawal AF. 2009 Purging the genome with sexual selection: reducing mutation load through selection on males. *Evolution* **63**, 569–582. (doi:10.1111/j.1558-5646.2008.00558.x)
46. Hollis B, Fierst JL, Houle D. 2009 Sexual selection accelerates the elimination of a deleterious mutant in *Drosophila melanogaster*. *Evolution* **63**, 324–333. (doi:10.1111/j.1558-5646.2008.00551.x)
47. Agrawal AF. 2001 Phenotypic plasticity in the interactions and evolution of species. *Science* **294**, 321–326. (doi:10.1126/science.1060701)
48. Siller S. 2001 Sexual selection and the maintenance of sexual reproduction. *Nature* **411**, 692–695. (doi:10.1038/35079578)
49. Lorch P, Proulx S, Rowe L, Day T. 2003 Condition-dependent sexual selection can accelerate adaptation. *Evol. Ecol. Res.* **5**, 867–881.
50. Candolin U, Heuschele J. 2008 Is sexual selection beneficial during adaptation to environmental change? *Trends Ecol. Evol.* **23**, 446–452. (doi:10.1016/j.tree.2008.04.008)
51. Miller CW, Svensson EI. 2014 Sexual selection in complex environments. *Annu. Rev. Entomol.* **59**, 427–445. (doi:10.1146/annurev-ento-011613-162044)
52. Martínez-Ruiz C, Knell RJ. 2017 Sexual selection can both increase and decrease extinction probability: reconciling demographic and evolutionary factors. *J. Anim. Ecol.* **86**, 117–127. (doi:10.1111/1365-2656.12601)

53. Servedio MR, Boughman JW. 2017 The role of sexual selection in local adaptation and speciation. *Annu. Rev. Ecol. Syst.* **48**, 85–109. (doi:10.1146/annurev-ecolsys-110316-022905)
54. Arbutnot D, Rundel HD. 2012 Sexual selection is ineffectual or inhibits the purging of deleterious mutations in *Drosophila melanogaster*. *Evolution* **66**, 2127–2137. (doi:10.1111/j.1558-5646.2012.01584.x)
55. Radwan J. 2008 Maintenance of genetic variation in sexual ornaments: a review of the mechanisms. *Genetica* **134**, 113–127. (doi:10.1007/s10709-007-9203-0)
56. Chenoweth SF, Appleton NC, Allen SL, Rundle HD. 2015 Genomic evidence that sexual selection impedes adaptation to a novel environment. *Curr. Biol.* **25**, 1860–1866. (doi:10.1016/j.cub.2015.05.034)
57. Martinossi-Allibert I, Rueffler C, Arnqvist G, Berger D. 2018 The efficacy of sexual selection under environmental change. *bioRxiv* (doi:10.1101/283457)
58. Kelly PW, Pfennig DW, de la Serna-Buzón S, Pfennig KS. 2019 Male sexual signal predicts phenotypic plasticity in offspring: implications for the evolution of plasticity and local adaptation. *Phil. Trans. R. Soc. B* **374**, 20180179. (doi:10.1098/rstb.2018.0179)
59. Shelley PB. 1840 A defence of poetry. In *Essays, letters from abroad, translations and fragments* (ed. M Shelley). London, UK: Edward Moxon.
60. Rigney D. 2010 *The Matthew effect: how advantage begets further advantage*. New York, NY: Colombia University Press.
61. Stanovich KE. 2008 Matthew effects in reading: some consequences of individual differences in the acquisition of literacy. *J. Educ.* **189**, 23–55. (doi:10.1177/0022057409189001-204)
62. Sokolova IM, Pörtner HO. 2003 Metabolic plasticity and critical temperatures for aerobic scope in a eurythermal marine invertebrate (*Littorina saxatilis*, Gastropoda: Littorinidae) from different latitudes. *J. Exp. Biol.* **206**, 195–207. (doi:10.1242/jeb.00054)
63. Somero GN. 2010 The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. *J. Exp. Biol.* **213**, 912–920. (doi:10.1242/jeb.037473)
64. Pörtner HO. 2002 Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* **132**, 739–761. (doi:10.1016/S1095-6433(02)00045-4)
65. Norin T, Metcalfe NB. 2019 Ecological and evolutionary consequences of metabolic rate plasticity in response to environmental change. *Phil. Trans. R. Soc. B* **374**, 20180180. (doi:10.1098/rstb.2018.0180)
66. Gaitán-Espitia JD, Bacigalupe LD, Opitz T, Lagos NA, Osorio S, Lardies MA. 2017 Exploring physiological plasticity and local thermal adaptation in an intertidal crab along a latitudinal cline. *J. Therm. Biol.* **68**, 14–20. (doi:10.1016/j.jtherbio.2017.02.011)
67. Gaitán-Espitia JD, Marshall D, Dupont S, Bacigalupe LD, Bodrossy L, Hobday AJ. 2017 Geographical gradients in selection can reveal genetic constraints for evolutionary responses to ocean acidification. *Biol. Lett.* **13**, 20160784. (doi:10.1098/rsbl.2016.0784)
68. Gaitán-Espitia JD, Villanueva PA, Lopez J, Torres R, Navarro JM, Bacigalupe LD. 2017 Spatio-temporal environmental variation mediates geographical differences in phenotypic responses to ocean acidification. *Biol. Lett.* **13**, 20160865. (doi:10.1098/rsbl.2016.0865)
69. Chevin L-M, Hoffmann AA. 2017 Evolution of phenotypic plasticity in extreme environments. *Phil. Trans. R. Soc. B* **372**, 20160138. (doi:10.1098/rstb.2016.0138)
70. Arnold PA, Nicotra AB, Kruuk LEB. 2019 Sparse evidence for selection on phenotypic plasticity in response to temperature. *Phil. Trans. R. Soc. B* **374**, 20180185. (doi:10.1098/rstb.2018.0185)
71. Bacigalupe LD, Gaitán-Espitia JD, Barria AM, Gonzalez-Mendez A, Ruiz-Aravena M, Trinder M, Sinervo B. 2018 Natural selection on plasticity of thermal traits in a highly seasonal environment. *Evol. App.* **11**, 2004–2013. (doi:10.1111/eva.12702)
72. Veilleux HD *et al.* 2015 Molecular processes of transgenerational acclimation to a warming ocean. *Nat. Clim. Change* **5**, 1074–1078. (doi:10.1038/nclimate2724)
73. Schunter C, Welch MJ, Ryu T, Zhang H, Berumen ML, Nilsson GE, Munday PL, Ravasi T. 2016 Molecular signatures of transgenerational response to ocean acidification in a species of reef fish. *Nat. Clim. Change* **6**, 1014–1018. (doi:10.1038/nclimate3087)
74. Schunter C, Welch MJ, Nilsson GE, Rummer JL, Munday PL, Ravasi T. 2018 An interplay between plasticity and parental phenotype determines impacts of ocean acidification on a reef fish. *Nat. Ecol. Evol.* **2**, 334–342. (doi:10.1038/s41559-017-0428-8)
75. Bernal MA, Donelson JM, Veilleux HD, Ryu T, Munday PL, Ravasi T. 2018 Phenotypic and molecular consequences of stepwise temperature increase across generations in a coral reef fish. *Mol. Ecol.* **27**, 4516–4528. (doi:10.1111/mec.14884)
76. Ryu T, Veilleux HD, Donelson JM, Munday PL, Ravasi T. 2018 The epigenetic landscape of transgenerational acclimation to ocean warming. *Nat. Clim. Change* **8**, 504–509. (doi:10.1038/s41558-018-0159-0)
77. Putnam HM, Davidson JD, Gates RD. 2016 Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. *Evol. Appl.* **9**, 1165–1178. (doi:10.1111/eva.12408)
78. Liew YJ *et al.* 2018 Epigenome-associated phenotypic acclimatization to ocean acidification in a reef-building coral. *Sci. Adv.* **4**, eaar8028. (doi:10.1126/sciadv.aar8028)
79. Johnson KM, Hofmann GE. 2017 Transcriptomics response of the Antarctic pteropod *Limacina helicina antarctica* to ocean acidification. *BMC Genomics* **18**, 812. (doi:10.1186/s12864-017-4161-0)
80. Evans TG, Pespeni MH, Hofmann GE, Palumbi SR, Sanford E. 2017 Transcriptomic responses to seawater acidification among sea urchin populations inhabiting a natural pH mosaic. *Mol. Ecol.* **26**, 2257–2275. (doi:10.1111/mec.14038)
81. Wong JM, Johnson KM, Kelly MW, Hofmann GE. 2018 Transcriptomics reveal transgenerational effects in purple sea urchin embryos: adult acclimation to upwelling conditions alters the response of their progeny to differential pCO₂ levels. *Mol. Ecol.* **27**, 1120–1137. (doi:10.1111/mec.14503)
82. Nicotra AB *et al.* 2010 Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* **15**, 684–692. (doi:10.1016/j.tplants.2010.09.008)
83. Dixon GB, Davies SW, Aglyamova GV, Meyer E, Bay LK, Matz MV. 2015 Genomic determinants of coral heat tolerance across latitudes. *Science* **348**, 1460–1462. (doi:10.1126/science.1261224)
84. Torda G *et al.* 2017 Rapid adaptive responses to climate change in corals. *Nat. Clim. Change* **7**, 627–636. (doi:10.1038/nclimate3374)
85. Hendry AP. 2016 Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *J. Heredity* **107**, 25–41. (doi:10.1093/jhered/evs060)
86. Pigliucci M. 2005 Evolution of phenotypic plasticity: where are we going now? *Trends Ecol. Evol.* **20**, 481–486. (doi:10.1016/j.tree.2005.06.001)