











Putting plasticity into practice for effective conservation actions under climate change

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J. M. Donelson ^{1,2,15} ✉, J. D. Gaitan-Espitia ^{3,4,15}, A. J. Hobday ^{5,15},
K. Mokany ^{6,15}, S. C. Andrew ⁶, S. Boulter ⁷, C. N. Cook ⁸, F. Dickson⁹,
N. A. Macgregor ^{10,11}, N. J. Mitchell ¹², M. Pickup¹³ & R. J. Fox ^{14,15}

Phenotypic plasticity may help species to persist in the face of rapid change, yet we lack a management-friendly framework for incorporating plasticity into conservation practice. Here we emphasize the importance of phenotypic plasticity for management—when and how it matters—and describe three challenges that currently impede its consideration in conservation management. We propose a common language and framework that can be applied by scientists and conservation practitioners that connects plasticity to management actions. Crucially, our framework considers plasticity through the lens of an organism’s ‘fit’ to its environment and how that fit will be impacted by climatic changes. Finally, we present a road map for developing tools to highlight where consideration of plasticity is valuable for effective management.

Pressure on natural systems from rapid environmental change is mounting faster than expected. Climate extremes are increasing in severity^{1,2} and recent and projected climate, ocean and cryosphere changes are outpacing historical trends³. These developments give rise to serious concerns about the productivity and security of ecosystem services^{4,5}, as well as the resilience of global ecosystems and their ability to support biodiversity^{6,7}. The emerging scientific consensus is that the adaptive potential of species in these ecosystems is insufficient to keep pace with the cumulative pressures that humans are placing on biological systems^{8–10}. If species cannot adapt to new environmental conditions populations will decline and ecosystems will suffer without intervention. Conservation practitioners and researchers are looking to understand alternative interventions and when it is appropriate to implement them¹¹.

Classic concepts around species’ responses to environmental change often focus on genetic adaptation as the result of natural selection acting on heritable variation and adaptive potential being restricted to the genetic variance needed to respond to selection (see lexicon in Box 1). However, a species’ ability to persist in place can come from either or both genetic adaptation and plasticity (adaptive capacity, as used in ref. 12). The speed with which genetic adaptation can occur is limited by the amount of genetic variation that is present in a population or the rate at which new variants can be introduced (for example, by mutation, recombination or gene flow) relative to the strength of selection. Phenotypic plasticity is an alternative mechanism by which organisms can adjust their behaviour, physiology and performance in the face of environmental change^{9,13,14} allowing them to ‘persist in place’ or ‘shift in space’^{15,16}. These phenotypic adjustments

¹ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia. ²College of Science and Engineering, James Cook University, Townsville, Queensland, Australia. ³The Swire Institute of Marine Science, School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China. ⁴Institute for Climate & Carbon Neutrality, The University of Hong Kong, Hong Kong SAR, China. ⁵CSIRO Environment, Hobart, Tasmania, Australia. ⁶CSIRO Environment, Canberra, Australian Capital Territory, Australia. ⁷Geography, Planning and Spatial Sciences, University of Tasmania, Hobart, Tasmania, Australia. ⁸School of Biological Sciences, Monash University, Clayton, Victoria, Australia. ⁹Australian Government Department of Climate Change, Energy, the Environment and Water, Canberra, Australian Capital Territory, Australia. ¹⁰Parks Australia, Canberra, Australian Capital Territory, Australia. ¹¹Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, UK. ¹²School of Biological Sciences, The University of Western Australia, Crawley, Western Australia, Australia. ¹³Greening Australia, Perth, Western Australia, Australia. ¹⁴Division of Ecology & Evolution, Research School of Biology, The Australian National University, Canberra, Australian Capital Territory, Australia. ¹⁵These authors contributed equally: J. M. Donelson, J. D. Gaitan-Espitia, A. J. Hobday, K. Mokany, R. J. Fox.

✉ e-mail: jennifer.donelson@jcu.edu.au

BOX 1

Building a standardized lexicon for plasticity

Acclimation. Phenotypic changes that occur within the lifetime of an individual that alter tolerance to environmental change. This term should be synonymous with adaptive phenotypic plasticity, but is often used to indicate that organisms have been habituated to particular environmental laboratory conditions.

Adaptation. (Verb) The evolutionary process by which a species increases its fitness; it is the result of natural selection acting on heritable variation over two or more generations (adaptation in the ‘biological’ sense). (Noun) A character state/trait that enhances the survival or reproduction of organisms that bear it, relative to alternative character states. See also climate change adaptation below.

Adaptive capacity. The ability of a species to cope with, adjust to and persist in varied environments either within a location or through dispersal to new locations^{91,109}. Plasticity can be one of the capacities that contributes to a species’ overall adaptive capacity.

Adaptive evolutionary potential. Genetic variance needed to respond to selection that can be assessed either by adaptive traits or fitness¹¹⁰.

Adaptive management. A structured, iterative process of decision-making that aims to reduce uncertainty over time via monitoring or experimentation¹¹¹.

Adaptive plasticity. Phenotype variation of an individual across environments that results in the production of a phenotype that is closer to the optimal value favoured by selection in a new environment⁴².

Adaptive response. Process by which an individual or species becomes better suited to its environment as a result of natural selection acting on either one or both of the processes of heritable phenotypic variation or phenotypic plasticity (see ref. 112). Adaptive evolution applies in cases where the response is due to heritable phenotypic variation.

Climate change adaptation. Adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities¹¹³. This includes a range of sub-terms, including ecosystem-based adaptation, which are approaches that involve the management of ecosystems to reduce the vulnerability of human communities to impacts of climate change such as floods, erosion, warming (adaptation in the ‘climate change management’ sense).

Evolutionary potential. The capacity of a biological entity (for example a species, population, trait) to evolve in response to environmental change¹¹⁴.

Evolutionary rescue. Process by which a population that would have gone extinct in the absence of evolution persists due to natural selection acting on heritable variation.

Fit. The match between an organism’s traits and its prevailing biotic and abiotic conditions. The term is deliberately chosen here to link to ‘individual fitness’ and the idea that organisms with a better fit will constitute a population with higher mean fitness¹¹⁵.

Genotype by environment interaction. The variation among genotypes in how they respond across environments, visualized as the magnitude of change over time of multiple individuals. Genotype by environment interactions are therefore a property of the population or collection of genotypes (see refs. 42,116).

Genotype. An organism’s complete set of genetic material (autosomal DNA plus organellar DNA). In a narrower sense, it can also be used to describe the alleles (or variants) of a gene carried by the individual.

Genomics. The study of the entirety of the genome, including the structure, function, evolution, mapping and editing of genomes.

Genetics. The study of genes, genetic variation and heredity in organisms. Genetics scrutinizes the functioning and composition of single genes, rather than the entirety of the genomes as in genomics.

Gene flow. The exchange of genetic material between populations as a result of interbreeding or other forms of genetic transfer (for example, horizontal gene transfer).

Genetic diversity. The total number of genetic characteristics in the genetic makeup of a species.

Genetic drift. A mechanism of evolution in which the allele (variants of a gene) frequencies in a population change over generations due to chance (rather than selection). Genetic drift occurs in all populations, but its effects are expressed most strongly in small populations as loss of genetic diversity.

Genetic rescue. A management intervention designed to increase genetic diversity and reduce extinction risk in small, isolated and frequently inbred populations by introducing individuals with novel genetic variation. See translocation below.

Genetic variation. The variation in alleles of genes in the gene pool of a species or a population. It provides raw materials for the natural selection. Types can be further defined by whether gene variants have an effect on fitness (adaptive) or are not (neutral).

Heritability. The amount of phenotypic variation in a trait that is due to genetic variation, and thus can be passed to offspring.

Inclusive fitness. The ability of an individual to transmit genes to the next generation, including genes shared with relatives—for example, altruistic behaviour and cooperation that benefits siblings.

Individual fitness. An individual’s success in terms of their contribution to the next generation. Can be quantified as the average contribution to the gene pool of the next generation made by individuals of a specified genotype or phenotype. The fitness of a genotype is manifested through its phenotype, which is also affected by the developmental environment. The fitness of a given phenotype can be different in different environments.

Phenotype (overall). The set of expressed characteristics or traits of an organism. An organism’s phenotype is a result of its genotype and the influence of environmental factors. Understanding the wholistic

(continued from previous page)

phenotype of an individual is often difficult, so one or more characteristics are often used as a proxy (that is, trait phenotype).

Phenotypic plasticity. The capacity of a genotype to render alternative phenotypes under different environmental conditions, more broadly considered as environmentally induced phenotypic variation¹¹. Phenotypic plasticity is therefore the property of an individual. Phenotypic variation may be adaptive (beneficial to fitness), neutral or non-adaptive (negative to fitness). Plasticity can be further defined depending on when it occurs in a life cycle (for example, developmental, reversible, transgenerational) or the type of trait that is changing (for example, behavioural, physiological).

Phenotypic variance. The total variance observed in a trait across individuals within a population.

Quantitative genetics. The study of traits that are influenced by many genes, where, as a consequence, phenotypes will vary continuously (rather than discretely, as occurs with traits controlled by few genes).

Resilience (climate). The capacity of (eco)systems to maintain function and structure, while also maintaining the capacity for adaptation and transformation.

Selection. The differential survival and reproduction of individuals due to differences in phenotype. Natural selection is a key mechanism of evolution, with change in heritable traits characteristic of a population over generations.

Translocation. Movement of individuals of a species by humans from one area to another, either within or outside of a species indigenous range. The main motivations for conservation translocations are: population restoration (reinforcement and reintroduction) and conservation introduction (ecological replacement and assisted colonization)^{117,118}; see ref. 119 for a discussion of the genetic implications of translocation. Translocations also occur unintentionally, and for reasons not associated with conservation. Types of translocation include^{117,119}:

- Augmentation: movement of individuals into a population of conspecifics.
- Introduction: movement of an organism outside its historical range (may also be called assisted colonization).
- Reintroduction: movement of an organism into a part of its native/historical range from which it has disappeared.

are often mediated through epigenetic changes that take place within and across generations (for example, DNA methylation^{17,18}). Thus, plasticity can allow rapid environmental change to be mitigated within the lifetime of individuals or across a small number of generations, before any genetic adaptation, reducing the risk of local extinctions^{19,20}. This can occur through simply ‘buying time’ for adaptation to follow and by exposing cryptic genetic variation to selection^{21–23}. Alternatively, plasticity can impede evolution by shielding genotypes from selection²¹ and, in exceptional cases, may even negate the requirement for genetic adaptation (for example, ref. 24). Plasticity can therefore increase or decrease the ‘fit’ of individuals within a population to an altered environment, consequently impacting species’ evolutionary potential²¹. However, despite the value of understanding plasticity and the increased attention paid to the role of genetic adaptation in natural resource management (for example, refs. 25,26), there has been limited integration of plasticity into models used in decision-making (for example, refs. 27,28) and a framework that explicitly considers plasticity is lacking. This constrains the potential of harnessing a core mechanism that underpins species’ adaptive capacity when planning conservation actions in a rapidly changing world^{20,29}.

Recent efforts^{12,15,30,31} have started to address the challenge of plasticity in biodiversity conservation and climate change vulnerability assessments. The framework developed by these studies considers plasticity as one of the three components that underlie the innate ability of species to cope/adjust to climate change (that is, the adaptive capacity^{12,15,31}). Despite this progress, the previous framework is mainly oriented to the assessment and the enhancement of adaptive capacity, aspects that are more intuitive for dispersal ability and genetic diversity (the other two adaptive capacity components^{15,31}) than for plasticity. Moreover, in this framework, plasticity is mainly considered for the persist-in-place adaptive capacity response pathway¹⁵, despite it being known that plasticity is also relevant for the shift-in-space adaptive capacity response pathway (for example, ref. 16). While the adaptive capacity framework offers a way to integrate plasticity into management, there are important challenges faced in this process related to the practical identification of whether and in what circumstances phenotypic plasticity is adaptive in nature^{13,32,33}, and how

plasticity can be used to inform and enhance conservation outcomes. Yet considering the phenotypic plasticity of populations during conservation actions, such as translocations, could assist in reducing unwanted ecological and evolutionary outcomes³⁴, such as the loss of anti-predator behaviours in populations housed in predator-free sanctuaries before reintroduction (for example, refs. 35,36). Rapid climate change demands innovative conservation actions with limited opportunities and time for testing a range of them³⁷. Conservation practitioners need tools to help determine the importance (or otherwise) of phenotypic plasticity in management, and support from scientists to maximize uptake of appropriate management considerations (see ref. 38).

In this Perspective, we draw on the expertise of scientists and conservation practitioners to discuss the key challenges and potential benefits of putting plasticity into practice. Specifically, our focus is on harnessing the innate plastic responses of species to achieve more effective conservation outcomes, rather than attempting to increase or decrease plasticity itself or the adaptive capacity of the species. We describe scenarios where considering plasticity has the potential to enhance natural resource management—that is, when, how and why best-practice management should also consider plasticity. We suggest that managers consider how environmental change will interact with an organism’s phenotype to potentially track change and maintain suitable phenotypes under future scenarios. For example, in the case of western swamp turtles translocated to novel wetlands in southwestern Australia as a response to climate change, the lack of plasticity exhibited in behavioural thermoregulation leads to reduced performance in cooler locations³⁹. This limited plasticity should be considered when selecting alternative wetlands and to inform the best timing for assisted colonization initiatives³⁹. Alternatively, plasticity may allow organisms to manage conflicting short-term selection pressures that occur due to climate-driven environmental variability. Such considerations of plasticity could give scientists and practitioners a common route to devise pragmatic management actions. Finally, we present a road map to better link biological research, conservation and natural resource management when putting plasticity into practice.

The fundamentals of plasticity

Phenotypic plasticity is traditionally considered to be a rapid response mechanism for individuals, allowing time for evolutionary adaptation at the population level⁴⁰. While the concepts of plasticity and adaptation are inherently linked, they can act at different levels and timescales. The first fundamental principle of plasticity is that it can act within an individual's lifetime, resulting from cellular and molecular changes that allow morphological, behavioural and physiological adjustments (Fig. 1). In contrast, adaptation occurs at the level of the population over multiple generations, as the outcome of selection on heritable phenotypic variation, and results in changes to genetic composition of the population⁴¹. The difference in how plasticity and adaptation operate, combined with the fact that plasticity can be heritable and under selection, makes the practical application of plasticity in conservation challenging.

Our theoretical understanding of the role that plasticity will play in eco-evolutionary processes with environmental change is well defined²¹. We understand that phenotypic plasticity is not a binary response of the organism to environmental change, but a continuum of many different traits from behavioural, to physiological, to the environmental niche and life-history characteristics. Furthermore, not all plastic changes are adaptive (that is, provide fitness benefits that are selected for⁴²). The direction of the plastic response can be positive, neutral or negative to fitness depending on the interaction between ecological processes, the degree and duration of environmental variation over time and organismal attributes^{43,44}. Trade-offs may also play a role, with a positive plastic response in one trait reducing other aspects of fitness (for example, increased thermal tolerance could reduce resources available for reproduction).

The impact of plasticity in terms of shifting individual phenotypes within the population may not always be apparent in the short term (Fig. 2). For example, when the plasticity of individuals can keep pace with environmental change, there are unlikely to be observable differences in genetic or phenotypic diversity in a population through time (time_{t+1}), independent of whether that plastic response is variable (genotype by environment interactions; 4 in Fig. 2) or all genotypes have similar plastic capacity (2 in Fig. 2). However, if the environment continues to shift, the population displaying variation in plasticity could experience a loss of genetic diversity due to selection favouring some genotypes over others, with associated conservation implications (time_{t+3}; 4 in Fig. 2). In the extreme case where plasticity results in an organism with a perfect fit to the new environment (2 in Fig. 2), plasticity can limit the process of genetic differentiation between populations, buffering selective pressures for adaptive evolution.

Not all organisms are equally capable of phenotypic plasticity due to intrinsic limitations in their genetic architectures^{45,46}. Plastic potential and adaptive outcomes can differ across a species' distribution, depending on the environmental context and the genetic structure of populations^{16,47}. The greatest potential to synthesize how plasticity and adaptation operate to bridge the current gap between theory and practice is offered through the link between plasticity and environmental change (Fig. 2). 'Change' (and its dimensions of predictability, magnitude, rate and directionality) is the primary underlying driver of plasticity. The nature of environmental change can influence if, when and how plasticity occurs within and across generations^{48–50}. The benefits (or otherwise) of plasticity will often depend on whether environmental change is stochastic or predictable in nature, such that stochastic changes and unreliable environmental cues can produce phenotypic mismatches, limiting the benefits of plasticity in natural populations^{51,52}. Predictable and directional environmental changes, together with well-aligned sensory and regulatory mechanisms, allow phenotypic change and can produce better phenotype–environment matches than would be possible for less- or non-plastic organisms⁵³. In environments with predictable variation, increased phenotypic

plasticity is favoured and plastic organisms have enhanced fitness (that is, tolerance or performance) under these conditions⁵². However, in cases of stochastic variation, phenotypic change can manifest through bet-hedging, where selection favours parents producing diversity in offspring phenotypes such that the population maintains fitness though some offspring phenotypes matching the future environments⁵⁴.

In many systems, climate change will be a predictable change (for example, gradual warming in average conditions³), resulting in high potential for both plastic and evolutionary responses to play a role. The frequency and severity of extreme events (for example, heatwaves, cyclones, flood events, drought) is increasing, which could be predictable or unpredictable depending on the system^{55,56}. In a less predictable world, the capacity of organisms to maintain good fit between environmental change and phenotypic change through plasticity is likely to be an important indicator of ecological resilience (population/species persistence) and thus a fundamental component of effective conservation. In subsequent sections we return to this idea of maintaining a fit with the environment under climate change (a directional trend with variability both predictable and unpredictable) and discuss practical solutions to the challenges of incorporating plasticity into conservation practice.

Challenges with putting plasticity in practice

Although the importance of phenotypic plasticity is theoretically intuitive, conceptual and practical challenges arise when trying to operationalize plasticity into conservation management. Some of these challenges are common to the interdisciplinary interface between science and management (see refs. 38,57), while others are unique to the peculiarities of plasticity. Below we identify three key challenges associated with putting plasticity into practice and offer potential solutions.

Challenge 1: miscommunication

In discussions of plasticity and adaptation, like other related eco-evolutionary concepts, scientists and decision-makers can have field-specific terms or use the same terminology for different things. One such example is the differing interpretations of adaptation, including within biological adaptation (all the composite terms) and its distinction from plasticity, versus climate change adaptation and adaptive management, which involve human management of biological systems (Box 1). This can give rise to ambiguity and limits effective communication between (and within) scientists and decision-makers. Where ambiguity exists in the communication of ideas it is difficult to move from research to action, and so a common and accessible lexicon is a critical step in operationalizing plasticity into management.

Solution 1: develop and apply a plasticity lexicon for scientists and practitioners

The translation of plasticity and eco-evolutionary concepts into management practice requires the development of a standard lexicon of terms. Ideally, these would be developed alongside guidance for practitioners, with a focus on clarifying the language and providing context as to why the concepts are important to understand. A full exposition of this practitioner-focused approach is beyond the scope of this Perspective, but we provide a minimum list of terms in Box 1.

Challenge 2: evidence for adaptive plasticity in nature is scarce

To make a case for considering plasticity as contributing to a population's or species' persistence under global change, plasticity must be shown to be adaptive. Without such evidence, there is understandable scepticism among many as to whether plasticity deserves explicit consideration. The empirical evidence for plasticity being adaptive is limited at present (see ref. 32), and there are several reasons why making an evidence-based case within nature is difficult. First, traits that are highly plastic tend to contribute little to overall measures of

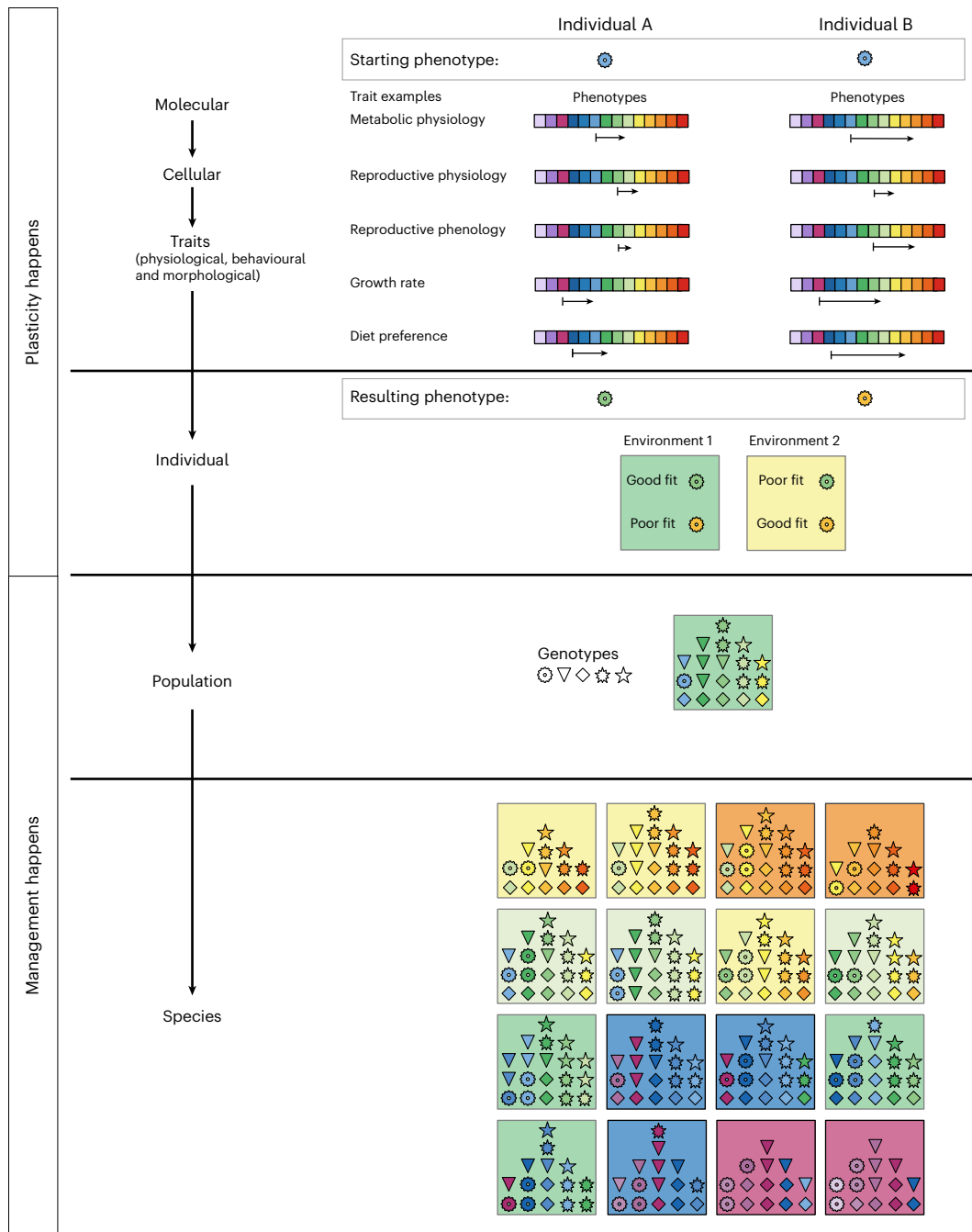


Fig. 1 | The fundamentals of phenotypic plasticity for a species. This scales up plasticity from the molecular to whole-organism level and shows its relevance at the population and species levels. Individuals A and B with the same genotype (shape) and starting phenotype (colour) differ in their levels of plasticity when environmental change is experienced. The plasticity of traits is indicated by the lengths of the arrows (greater plasticity is indicated by longer arrows). This results in differing phenotypes that can have either a poor or good fit to the prevailing environment, indicated by the extent to which an individual’s colour matches the environment (the background colour of the square). Within a population, individuals will have a range of phenotype

by genotype combinations that fit the environmental condition (colour and shape combinations similar to the background environmental colour). Across populations of a species there will be heterogeneous environmental conditions (shown by the 16 squares of differing colours), and varying phenotype by genotype distributions. The distribution of phenotypes, either within or across populations, can be used to understand both the current fit between phenotypes and the environment, and how the fit might alter with environmental change. Considering the fit across populations can be used as a method to prioritize conservation.

fitness^{13,58,59} (but see ref. 33). In addition, the role that plasticity plays in adaptive processes can be masked by genetic differentiation acting in either the same⁶⁰ or opposing⁵⁸ directions to plasticity. In such cases, the influence of plasticity in adaptive processes may be revealed only under conditions of more extreme or persistent environmental change. Similarly, adaptive plasticity can be masked by reductions in growth- or

size-related traits typically associated with low-quality environments and once these allometric relationships are controlled for, the contribution of plastic trait responses to higher fitness may be revealed⁶¹.

Finally, in novel environments, plastic traits more closely related to fitness are predicted to be under stronger selection for genetic canalization^{62,63}. The process of canalization essentially involves the

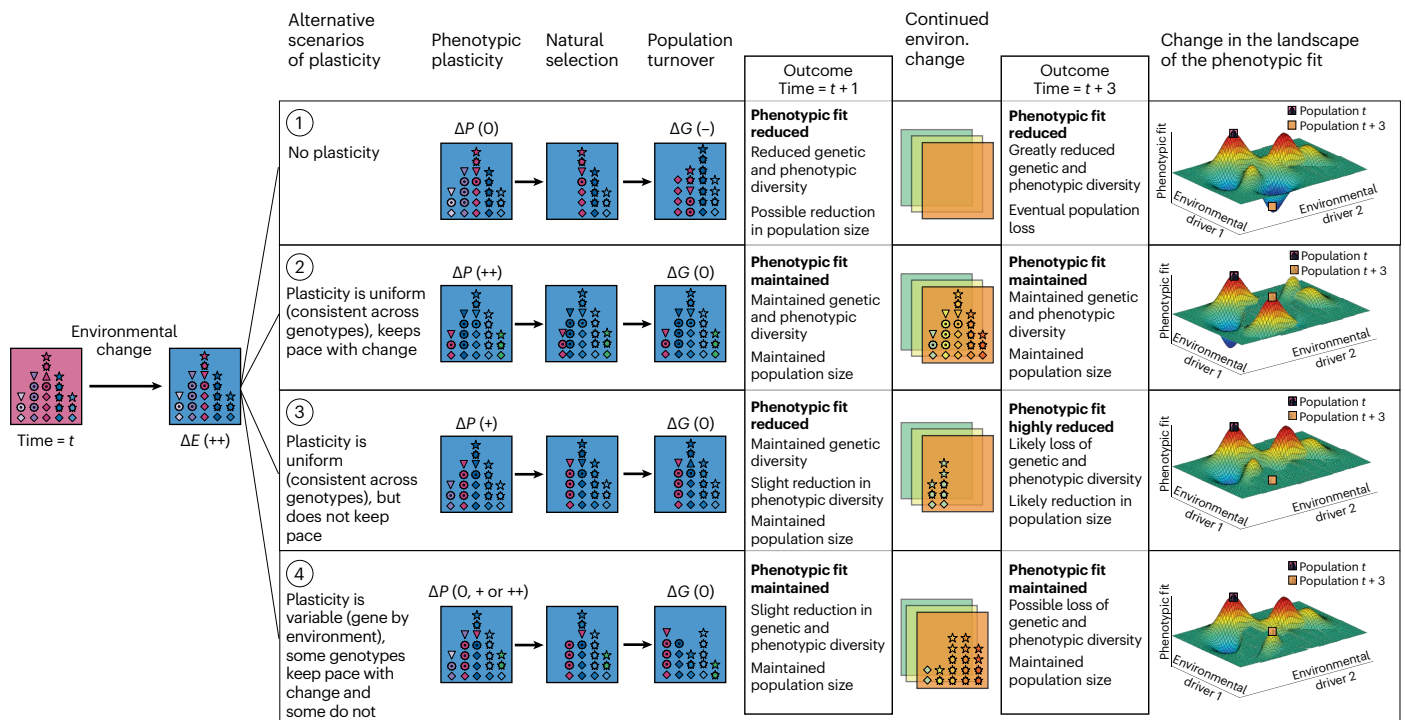


Fig. 2 | The nature of plasticity matters in response to rapid environmental change. Four alternative scenarios are shown for a single population through time with the expected outcomes as the environment directionally changes: (1) no plasticity; (2) plasticity is uniform (consistent across genotypes) and able to keep pace with the rate of environmental change (ΔE); (3) plasticity is uniform (consistent across genotypes) but not able to keep pace with the rate of ΔE ; and (4) plasticity is variable (genotype by environment interactions) where the plasticity of some genotypes keeps pace with change while others do not. As in Fig. 1, shapes indicate genotypes and colours indicate phenotypes. ΔG , change in genotypic diversity; ΔP , change in phenotypic diversity. Working horizontally, as the environment shifts (box colour changes), each scenario steps through time in a hypothetical population. Here we provide differing expectations of

phenotypic fit, phenotypic and genetic diversity, and population size shifts through time with continued environmental change. The far-right panels visualize each scenario in a three-dimensional landscape, with the population at starting time t highlighted with a purple box and the population at $t + 3$ with an orange box, and two components of environmental change. Plasticity is shown by whether populations can shift to a different peak (or not) as the environment changes. In scenario 3 (scenarios 2 and 4 are discussed in text), uniform plasticity is possible across genotypes, but the plasticity does not accommodate the amount of environmental change experienced. This results in a reduced fit of the population through time ($t + 1$), which is amplified as the environment continues to change directionally ($t + 3$). This results in the population not able to maintain a peak in phenotypic fit.

‘assimilation’ of non-heritable, environmentally induced variation into heritable variation (also known as genetic assimilation⁶⁴). As part of this process, traits that were previously environmentally determined become genetically determined and can result in a loss of plasticity and the organism showing a flat reaction norm⁴². The broader term genetic accommodation, which contains genetic assimilation⁶⁴, can include heritable variation occurring in the same direction as plastic responses and does not have to lead to a loss of plasticity¹⁴. The end point of canalization can manifest as a non-adaptive reaction norm, and with future environmental change may be interpreted as a case of no evidence of plasticity (i) in Fig. 2, potentially leading to an underestimation of the role that plasticity may have played in the initial stages of organisms adapting to their environment.

Solution 2: flipping the focus

To argue that the adaptive importance of plasticity is unproven is not useful in progressing conservation policy and decision-making. In light of the rapid rate, diversity and magnitude of projected climate change, we do not have the luxury of waiting for experimental evidence to fall unequivocally on one side or the other, as we face the risk of mass extinction^{65,66}. Hence a pragmatic way forwards is to clarify why plasticity matters and when it is possible for decision-makers to assume that plasticity will play a role in conservation actions. It is also important to provide managers with an understanding of how plasticity may be considered in decision-making and integrated into

adaptive management practices. In this way, we can expand and enrich the existing adaptive capacity framework¹⁵, with the aim of developing more practical tools and critical thinking for planning conservation and management efforts.

Flipping the focus requires identifying circumstances under which considering plastic capacity might be valuable for effective conservation management. This might include cases where evolutionary adaptation through experimental manipulation does not produce enhanced performance⁶⁷ and selecting for plasticity may provide evolutionary rescue⁶⁸, or where human management actions alter survival (for example, assisted recruitment, or harvesting) or inadvertently affects future adaptive potential by altering natural selective processes^{34,69,70}. It could also include cases where the risks associated with not considering plasticity could be high (for example, the huge costs involved in ecological restoration⁷¹) and where consideration of plasticity renders action unnecessary, meaning that conservation resources could be directed elsewhere. For example, plasticity in foraging strategies and behavioural thermoregulation in pika, *Ochotona princeps*, allowed the species to naturally adjust to atypical environmental conditions in low-elevation habitats⁷². However, the capacity for managers to use knowledge on plasticity requires it to be fit for management so that can better support evidence-based decision-making.

To illustrate how plasticity matters in practice (that is, in terms of effect on conservation outcomes), we highlight examples from peer-reviewed literature of four possible scenarios in conservation









	Plasticity not considered	Plasticity was considered	
Plasticity did matter	<p>1</p> <p>Negative effect on conservation</p>  <p>Kakapo (<i>Strigops habroptilus</i>)^{73,74}</p> <p>Due to being critically endangered, supplemental feeding was provided to females to increase breeding frequency. Females plastically adjusted the sex-ratio of their broods in response to supplemental feeding resulting in a surplus of males.</p>  <p>Monarch butterfly (<i>Danaus plexippus</i>)⁹⁹</p> <p>Captive rearing and release of butterflies has been completed historically in North America for a number of reasons, including to assist with population recovery. However, captive breeding within indoor locations causes essential migratory orientation behaviour to be lost. Work has shown that behaviours can be conserved if butterflies are reared outside in natural conditions.</p>  <p>Atlantic salmon (<i>Salmo salar</i>)¹⁰⁶</p> <p>Stocking programmes are used to supplement natural reproduction for Atlantic salmon in Lake Ontario, Canada. Hatchery-reared fish had reduced survival, but fish that survived exhibited similar migration behaviour.</p>	<p>2</p> <p>Positive effect on conservation</p>  <p>Northern quoll (<i>Dasyurus hallucatus</i>)^{75,76}</p> <p>The reintroduction of quolls into Kakadu National Park was undertaken to prevent local extinction. The exploitation of behavioural plasticity to develop quoll populations that are 'toad smart' and less likely to prey on poisonous introduced cane toads was effective. However, additional training to avoid predators (dingos) was not successful.</p>  <p>Redside dace (<i>Clinostomus elongatus</i>)¹⁰⁵</p> <p>To inform reintroduction strategies, the thermal tolerance of three geographic lineages was explored. Lineages display variation in plasticity of critical thermal maximum, resulting in the central region having a thermal safety margin that was twice as high should be accounted for when selecting source populations for reintroduction.</p>  <p>Yellow-naped Amazon (<i>Amazona auropalliata</i>)¹⁰²</p> <p>Reciprocal translocation of birds from farming to ranching areas, which differ in habitat composition and vegetation, was conducted. Birds displayed plasticity in ranging and roosting behaviours to habitat composition allowing them to match resident bird behaviours.</p>	
	Plasticity did not matter	<p>3</p> <p>Neutral effect on conservation</p>  <p>Invasive American bullfrog (<i>Lithobates catesbeianus</i>)¹⁰⁷</p> <p>Seasonal draining programmes of managed wetlands to kill off invasive larvae are common practice in the Pacific Northwest. The plasticity of invasive larvae in the form of rapid metamorphosis to hydroperiod could have undermined the conservation action, but it was confirmed post hoc that invasive larvae did not show plasticity in their growth and development rates.</p>	<p>4</p> <p>Neutral effect on conservation</p>  <p>British white-clawed crayfish (<i>Austroptamobius pallipes</i>)¹⁰⁸</p> <p>The translocation of individuals from populations that differ in environmental conditions can reduce survival. Crayfish from stream and pond habitats differed morphologically due to source habitat. When translocated to ponds, crayfish from stream populations exhibited plasticity through increased carapace and areola width. However, this plasticity did not result in differences in survival or growth compared with control or reciprocally translocated crayfish from ponds to streams.</p>

Fig. 3 | Matrix of scenarios based on whether plasticity affected outcomes of conservation activities. Four scenarios are shown: whether plasticity mattered to conservation but was not considered^{73,74,99,105} (1); plasticity mattered and was considered^{75,76,102,106} (2); plasticity was not considered and did not matter in practice¹⁰⁷ (3); and plasticity was considered but did not matter in practice¹⁰⁸ (4). Credit: Photographs in (1), kakapo, NZ Department of Conservation under a Creative Commons license [CC BY 2.0](https://creativecommons.org/licenses/by/2.0/); monarch butterfly, Bernard Spragg under a Creative Commons license [CC0 1.0](https://creativecommons.org/licenses/by/1.0/); Atlantic salmon, CSIRO under a Creative

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management: (1) plasticity mattered but was not considered; (2) plasticity mattered and was considered; (3) plasticity was not considered but did not matter; and (4) plasticity was considered but did not matter in practice (Fig. 3). Of these four scenarios, (1) and (4) are clearly of greatest concern in terms of their potential to generate either sub-optimal conservation outcomes or wasted investment. Less evidence for scenarios (3) and (4) may in part be due to publication bias towards cases when plasticity matters, or the fact that plasticity could not be distinguished from genetic adaptation. In contrast, there are many examples where plasticity was not accounted for but did matter in terms of conservation outcomes (1). For instance, conservation actions for the Critically Endangered kakapo (*Strigops habroptilus*) failed to consider that supplementary feeding causes females to produce sex-biased broods, resulting in all-male offspring and a problematic population sex ratio^{73,74}. Cases in which plasticity is important and has been accounted for in management actions or planning (2) include the exploitation of behavioural plasticity to attempt to re-establish populations of the Endangered northern quoll (*Dasyurus hallucatus*) that are less likely to prey on poisonous introduced cane toads (*Rhinella marina*)^{75,76} (Fig. 3). Taken together, these highlight that managers should be planning for plasticity, consistent with a precautionary approach.

Challenge 3: no agreed-on framework for measuring plasticity or assessing likely benefits

Managing genetic adaptation, while challenging, is made possible because quantifiable metrics related to genetic diversity (for example, rates of polymorphism, proportion of polymorphic loci, number of alleles, allelic richness) can be readily monitored in free-living populations. One fundamental challenge faced when putting plasticity into practice is an absence of an equivalent single metric and the challenges of measuring plasticity across a diversity of realistic (and relevant) environmental conditions. However, seeking summary metrics for overall plasticity is a distraction for two reasons. First, the nature of plasticity is highly variable among taxa and traits: the method used to measure the plasticity of a trait depends on the trait itself and developing metrics is likely to be difficult. Second, there is also variation in how researchers study plasticity, and how conservation practitioners seek to apply the concept. For example, researchers often investigate the fitness consequences of a specific trait shift with environmental conditions and through time, whereas managers need information on both the present and the future to estimate how a species or population will respond to anthropogenic and environmental pressures.

Solution 3: develop a 'phenotype–environment fit' framework

Instead of seeking representative metrics of plasticity, a more pragmatic approach is to identify which traits need to be plastic for species to have maximum opportunity to show high adaptive capacity with respect to environmental change. How can we assess adaptive capacity by considering plasticity at the population- or species-level? One approach is the attribute-based framework for evaluating adaptive capacity developed by Thurman and colleagues^{15,31}. Under this framework, two general classes of adaptive responses are considered to identify effective management actions and develop adaptation strategies under climate change: persist in place and shift in space. These responses are underpinned by a set of common attributes ($n = 36$) that encompass higher-level characteristics such as distribution, movement, ecological role, abiotic niche, life history, demography and evolutionary potential. Plasticity could play a role in many of these attributes¹⁵. Building on this framework, we focus on adaptive capacity traits in which plasticity can play an extensive role and those that managers are likely to be able to estimate (Table 1). Many of these traits overlap with core attributes in ref. 31 (for example, range size/extent of occurrence, climatic niche breadth, physiological tolerance) or are a combination of their traits for simplicity (ecological flexibility

includes diet breadth, habitat specialization, commensalism with humans; reproductive flexibility includes reproductive mode and reproductive phenology). We propose that the degree of plasticity of these attributes can be assessed to estimate the phenotype–environment fit of species and populations through time to infer adaptive capacity. By estimating fit on timescales relevant to management, this provides a practical way forwards for conservation actions and implementation into species vulnerability assessments⁷⁷ alongside current adaptive capacity estimates³¹.

The phenotypic fit approach considers the interplay between the current sensitivity of individuals to environmental change and the potential for evolutionary and plastic processes through time (Fig. 2). In this framework, we do not suggest that genetic adaptation is ignored, simply that emphasis is given to the capacity of the species/populations to keep pace with environmental change through plastic adjustment of attributes that enable them to persist in place or shift in space. For this, we can visualize the different scenarios described in Fig. 2 through a phenotypic fit landscape. Here, the outcome of the interplay between plasticity and environmental change across time is conditioned by the alignment between the individual fitness of the organisms in a population, their trait values (that is, character states) and the prevailing biotic and abiotic conditions. Good alignments maintain populations at the hills of the landscape, while mismatches can push populations to valleys of phenotypic fit where genetic and phenotypic diversity are reduced with consequences for population size and long-term persistence.

This approach is consistent with other efforts, such as understanding phenotypic differences (that is, phenotypic diversity) across a species' range. For example, meta-analyses in some taxa identify attributes that seem to be limiting current distributions⁷⁸, or which will determine likely future persistence⁷⁹. However, we lack insight into how a given population can shift phenotypes through time, and whether this rate of shift can match the projected environmental change. Recently, Gauzere and colleagues⁸⁰ explored these uncertainties in a process-based model (PHENOFIT), validated with European tree species. Their model predicted that all species have plastic capacity in budburst date that would assist in adapting to climate change; however, in deciduous species (beech and oak) plastic capacity was insufficient to maintain optimal fit as the climatic conditions varied across elevations⁸⁰. This work illustrates that a narrow trait-based approach ignores the full role of plasticity under changing environments, where the fitness landscape will be changing simultaneously. It also highlights how taking plasticity into account can shift expectations of a species' response to climate change and allow managers to focus their short and long-term efforts.

Unfortunately, process-based modelling⁸⁰ will not be possible for most species. It requires data on functional traits and their relationship to fitness, which usually require long-term studies or many experimental manipulations. There are several alternative approaches that can be used as a starting point for attribute-based assessment (for example, refs. 77,81,82). Here we take a refined assessment of attributes recently proposed for measuring species' adaptive capacity¹⁵ and emphasize the additional consideration of plasticity and 'fit to future environment' (Table 1). From this, adaptive capacity is estimated on the basis of indicator traits and the risk level (that is, narrow or broad) associated with each trait. The critical differentiation for this framework is the incorporation of environmental context, with fit to future environment being the complementary information allowing for the more explicit consideration of plasticity. Here future fit is the assessment of how intrinsic ability will translate in practice in the novel environment. The difference is subtle, yet important. A robust approach would use data for many attributes when assessing phenotypic fit, although there will be some circumstances in which focusing on a single trait known to relate strongly to population sustainability and fitness will be sufficient, usually in cases where a species is well studied (for example, male fertility in *Drosophila*⁷⁸ or bleaching thresholds in corals⁸³).

Table 1 | Candidate attributes for determining current and likely future phenotypic fit to the environment

Phenotypic fit attribute		Indications of current phenotypic fit		Expectation of future phenotypic fit relative to degree of environmental change through a given time (allowing for stochastic variation)	Example
		Broad	Narrow		
Climatic niche breadth	Range of environmental conditions experienced by all life stages of a species	Wide niche breadth may indicate phenotypic flexibility to maintain fit	Restricted niche breadth may indicate constraints to phenotypic flexibility to maintain fit	Forecast environmental change is likely to lie outside the current climatic niche/range=negative expectation	Terrestrial-breeding <i>Geocrinia alba</i> frogs have a narrow niche breadth, with low tolerance to drying and high temperatures across life stages. Owing to this, and the projected drying climates in the future, further range contractions are expected for this species ⁸⁸ .
			Forecast environmental change is likely to lie within the current climatic niche/range=neutral or positive expectation	Where there is evidence that climatic niche breadth can shift to maintain fit=positive or neutral expectation	
Range size of extent of occurrence	The geographic coverage of the species range	Wide geographic range may indicate broad phenotypic fit, but should also be considered in conjunction with climatic niche breadth	A small range size may indicate a narrow phenotypic fit, but should also be considered in conjunction with climatic niche breadth	Contraction of species range through time could indicate reducing fit=negative expectation	Bird species with larger range sizes (broad) have been more successfully introduced to areas outside their indigenous ranges. However, some of this pattern may be due to the suitability of the abiotic environment at the introduction location and greater introduction efforts for large-range-size species ⁸⁹ .
			Expansion of species range through time could indicate increasing fit=positive expectation	No change=neutral expectation	
Range position	The location of a population within the indigenous species range. This range position can be assessed latitudinally or altitudinally. Trailing edge: populations living at the warm limits of a species range (lower latitude and elevation). Core: populations in the central region of a species range. Leading edge: populations living at the cool limits of a species range (higher latitude and elevation).	Populations located at the leading edge of a species' range can indicate that populations are not living close to their upper tolerance for certain environmental conditions Core locations can indicate that populations occur well within the bounds of environmental factors that limit persistence	Populations located at the trailing edge of the species range can indicate that populations are close to their upper limits of physiological tolerance for certain environmental conditions, such as temperature	Trailing edge populations can have declining fit with warming=negative expectation	
			Leading edge populations size can have increasing fit with warming=positive expectation	Insects (butterflies and grasshoppers) occurring at mid elevations have higher fitness (fecundity and survival) than leading-edge or trailing-edge populations. The fecundity (but not survival) of leading-edge populations is expected to increase under climate change (according to models based on empirical data, including thermal performance curves ⁹⁰).	
Population growth	Rate of change in the number of individuals within a population	Growing populations may have sufficient genetic and phenotypic diversity	Declining populations may have reduced genetic and phenotypic diversity	Decreasing population size with environmental change may indicate reducing fit=negative expectation Increasing population size with environmental change may indicate greater capacity to produce plastic and/or adaptive change=neutral expectation Increasing population size with environmental change may indicate increasing fit=positive expectation	Damselfly populations with higher growth rates also had greater colour polymorphism (phenotypic diversity). The mechanism is likely to be the reduction of female harassment by males seeking to mate with particular colour morphs ⁹¹ .
Physiological tolerance	Range of environmental conditions in which individuals can maintain survival and performance	Wide physiological tolerance breadth may indicate phenotypic flexibility to maintain fit	Limited physiological tolerance breadth may indicate constraints on phenotypic flexibility	Forecast environmental change is likely to lie outside the bounds of the current breadth=negative expectation Forecast environmental change is likely to lie within bounds of the current breadth=neutral or positive expectation Where there is evidence physiological tolerance can shift to maintain fit=positive or neutral expectation	Field and laboratory experiments showed that, contrary to predictions, species of salamander within the <i>Plethodon jordani</i> complex could shift physiological tolerances through acclimation to warming conditions via adjustment of water loss rates and metabolic rates ⁸⁴ .

Table 1 (continued) | Candidate attributes for determining current and likely future phenotypic fit to the environment

Phenotypic fit attribute		Indications of current phenotypic fit		Expectation of future phenotypic fit relative to degree of environmental change through a given time (allowing for stochastic variation)	Example
		Broad	Narrow		
Sensitivity to stressor(s)	Use of historical response to environmental stress. Could be monitored by growth, mortality fecundity	Evidence of robustness to previously experienced stressors	High sensitivity to previously experienced stressors	Forecast environmental change is likely to lie outside the bounds of the current range=negative expectation	In the case of soil microorganisms (bacteria and fungi), it has been shown that the past drought history impacts the current diversity and biomass under drought conditions. During new drought, the abundance of some microorganisms decreased in historically droughted soils (narrow), while many bacteria increased (broad) and the alpha diversity of bacteria increased, suggesting that historical responses to environmental stress can be used as predictors of future responses ⁹² .
				Forecast environmental change is likely to lie within the bounds of the current range=neutral or positive expectation	
				Where there is evidence sensitivity can shift to maintain fit=positive or neutral expectation	
Ecological flexibility	Specificity in ecological requirements (for example, symbiosis, diet flexibility, nesting and breeding flexibility)	Generalist ecology may indicate high phenotypic flexibility to maintain fit	Specialization may indicate reduced phenotypic flexibility to maintain fit	Forecast environmental change is likely to lie outside the bounds of the current fit=negative expectation	Species of birds that show more innovation/greater behavioural flexibility (broad) are at lower risk of global extinction (meta-analysis ⁹³).
				Forecast environmental change is likely to lie within the bounds of the current fit=neutral or positive expectation	
				Where there is evidence ecological flexibility can shift to maintain fit=neutral or positive expectation	
Reproductive flexibility	Phenology (flexibility in the timing of reproductive events) Reproductive mode can change, depending on weather conditions	Wider range of reproductive timing seasonally or lability in reproductive modes may indicate broader phenotypic fit.	Limited reproductive window possibly related to climatic, lunar or biotic cues, may indicate narrowing of phenotypic fit under future conditions. Reproductive mode is fixed.	Forecast environmental change is likely to lie outside the bounds of the current fit=negative expectation	Tortoises facultatively shifted from oviparity (eggs laid in nests) to ovoviviparity (eggs retained in oviducts until maturation) in response to hot summers, which probably buffered embryos from heat stress ⁹⁴ .
				Forecast environmental change is likely to lie within the bounds of the current fit=neutral or positive expectation	
				Where there is evidence reproductive flexibility can shift to maintain fit=neutral or positive expectation	

Attributes identified are adaptive capacity traits in which plasticity can play an extensive role and those that managers are likely to be able to estimate. Each attribute is considered here in terms of its current phenotypic fit and what values would indicate a broad or narrow fit (on a relative scale), as well as potential evidence for a shift in future fit (see Solution 3). A negative expectation is when a phenotype becomes less suited to future environmental conditions, a positive expectation is when a phenotypic fit will probably increase, while a neutral expectation is when a phenotypic fit is likely to be maintained under future environmental conditions.

In general, traits relating to reproduction and recruitment are likely to be key candidate attributes and are often a focus in monitoring programmes for threatened species.

A fundamental aspect of our proposed approach to managing species' plasticity in response to climate change considers the 'environment through time'. Time is important in terms of considering the nature and pace of environmental change, and the rate at which phenotypes may be able to shift and therefore the fit maintained. The perspective of time can be important in cases when plasticity was not planned for, but probably affected the conservation outcome, such as the red-cheeked salamander⁸⁴. The knowledge that this species complex had a relatively broad physiological tolerance (broad phenotypic fit attribute, Table 1) could be used to indicate that the salamander was likely to maintain a good fit to its environment under warming

conditions, and consequently plasticity-related management actions are unlikely to be necessary⁸⁴.

A road map for putting plasticity into practice

Given the potential for plasticity to alter the effectiveness of conservation actions, practitioners need clear guidance on how to incorporate consideration of plasticity into existing population management activities. A key feature of such guidance will be indicating circumstances under which benefits will probably arise from considering plasticity, and similarly where plasticity can be ignored. Given that gaps in our knowledge of organism plasticity will remain, it is important to embed conservation actions in adaptive management cycles and include procedures for collecting data related to plasticity when implementing conservation actions. The evaluation of such data would enable

Table 2 | Example conservation management actions and their potential to incorporate planning for plasticity

Management actions	Example	Ecological–evolutionary processes affected	Examples where plasticity has an impact	Ways for management actions to take account of future phenotypic fit
(a) Direct strategies that relate to species management				
Removal of threats	Management or removal of invasive species	<p>The removal of key species can alter species interactions, competition and ecological niches outside the direct intention of the activity.</p> <p>The addition of invasive or non-native species can alter community interactions.</p> <p>Invasive species often have higher plastic capacity than native species, in support of the hypothesis that invaders are generally more plastic for traits affecting fitness in ecologically relevant environments^{95,96}.</p>	<p>Individuals of the native North American butterfly, <i>Euphydryas editha</i> switched (via plasticity) to use the introduced exotic host plant <i>Plantago lanceolata</i> for oviposition. Offspring survival was increased on the exotic host species and over time the butterflies that used the native host were selected against and the population become dependent on the introduced plant species. When the availability of the introduced <i>Plantago</i> declined due to human action (changes in land management practices), the butterflies became locally extinct⁹⁷.</p>	<p>Management strategies for removal of invasive species should recognize that they may be better able to survive and adapt to changes in resource availability due to a more generalist niche and/or greater plasticity.</p> <p>Understanding the phenotypic fit of invasive species relative to that of relevant native species (for example, behavioural and ecological flexibility, or relative physiological tolerances) could help devise removal approaches that do not lead to undesirable side-effects.</p>
Harvesting	Removal of individuals from a wild population for human consumption, trophies or products.	<p>Can induce non-natural selection depending on the method or equipment used.</p> <p>Selection for certain phenotypes reduces population phenotypic diversity and/or skews the phenotypic distribution.</p> <p>The removal of particular phenotypes can induce plasticity within the remaining individuals (for example, sex change, growth plasticity, behavioural plasticity).</p>	<p>Fishing practices tend to select for specific phenotypes. For example, trawling for cod tends to select for fish above a threshold size and results in early maturation, except when fishing effort is low and confined to mature fish⁹⁸. In contrast gillnets, where small and large fish escape, can lead to late maturation for low to moderate harvest rates, but when harvest rates increase, maturation age drops⁹⁸. In species with sex change (for example, sequential hermaphroditism) incorrectly set size-based harvesting restrictions could affect population replenishment (fecundity) if the operation sex ratio becomes skewed.</p>	<p>Facilitate the use of a broad range of capture techniques to retain phenotypic diversity.</p> <p>Shift size limits in relation to phenotypic shifts in maturity.</p> <p>In cases of environmental change/stress, altering harvesting practices could enhance phenotypic diversity (that is, plastic and adaptive capacity to cope with current and future environmental change).</p>
Translocation (both within and outside a species' indigenous range) of wild individuals	<p>Introduction of individuals of a species at risk of extinction to an area outside of their typical range.</p> <p>Translocation of part of a population to avoid a specific environmental threat (either press/long-term or pulse/short-term event).</p>	<p>Translocation can provide new/novel genetic and phenotypic diversity.</p> <p>Translocation can increase population sizes via augmenting genetic diversity and creating more populations.</p> <p>Translocation outside a species indigenous range, or reintroduction to a location where a species has been locally extinct for some time, can create new and novel species interactions.</p>	<p>Naive northern quolls underwent behaviour training to develop a taste aversion to toxic invasive toads before translocation to locations with cane toads. Survival due to reduced toad consumption of trained individuals increased compared with non-trained individuals. However, additional training to avoid predators (dingos) was not as successful³⁵.</p>	<p>Consider the ecological flexibility of the focal species before movement of individuals, to try and limit unintended consequences of an introduction.</p> <p>Consider whether differences exist between the source and recipient populations in terms of physiological tolerance, reproductive biology, phenology and mating patterns (for example, sexual selection) that could result in enhanced success of translocations.</p> <p>Consider the number of individuals to be translocated as a way to reduce the risk of negative outcomes.</p>
Captive breeding for translocations	<p>Captive breeding programmes for species that would otherwise go extinct.</p> <p>Captive breeding and subsequent release into the wild of individuals for human consumption.</p> <p>Banking of species as insurance against future extinction risk such as seed banks.</p> <p>Genetic or phenotypic selection of individuals with particular traits that facilitate survival in a new environment or habitat.</p>	<p>Modified genetic and phenotypic diversity, with the hope of improved fitness in certain conditions.</p> <p>Individuals living in captivity can lose traits that are important for survival in the wild, creating problems for the use of captive animals for conservation³⁴.</p> <p>If an action involves breeding individuals to suit a particular environmental condition, induced selection may reduce plastic capacity to cope with novel environmental conditions.</p> <p>Artificial selection as part of breeding plants for reintroduction needs to ensure that seed is also suitable for the wild.</p>	<p>Captive rearing of monarch butterflies has often occurred indoors for conservation and education purposes. It was discovered that when early life development occurs indoors, even if the natural environment is mimicked, it alters the normally southern orientated migratory behaviour. When captive rearing occurred outside, the normal behaviour was restored⁹⁹.</p>	<p>Reintroduction of individuals should maximize genetic and phenotypic diversity, especially when the recipient population is small.</p> <p>For many species, captivity has the potential to alter the phenotype of individuals in ways that may not benefit fitness in the wild (for example, habituation). Quantification of the phenotypic diversity of individuals before release (for example, bold versus shy, reproductive phenology, physiological tolerance) or the phenotypes of key traits could allow the selection of adaptive traits. Training or cycling of individuals could also limit captivity effects.</p> <p>Consider how introduced individuals will be suited to future conditions at the location, as in western swamp tortoises (for example, ref. 100).</p>

Table 2 (continued) | Example conservation management actions and their potential to incorporate planning for plasticity

Management actions	Example	Ecological–evolutionary processes affected	Examples where plasticity has an impact	Ways for management actions to take account of future phenotypic fit
(b) Indirect strategies related to protection and management of species				
Spatial management (construction, addition or extension of protected areas)	<p>Improving the management of existing protected areas to facilitate resilience.</p> <p>The addition of protected areas can increase the genetic and phenotypic diversity of population networks.</p>	<p>Spatial management can influence reproductive output and effective population size.</p> <p>Redrawing boundaries may influence source–sink population dynamics by inclusion of either the source or sink within protected areas.</p> <p>Addition of protected areas.</p>	<p>For large terrestrial carnivores, natural habitats can be restricted to small protected areas within human-dominated landscapes. Habitat preferences and use by African lions (<i>Panthera leo</i>) are plastic depending on environment conditions including the proximity to water, prey abundance and anthropogenic pressures in the landscape surrounding protected areas. Plasticity can inform conservation in both current and future human-impacted landscapes¹⁰¹.</p>	<p>The selection or development of protected areas could take into account attributes of likely future fit, such as range position. This would require knowledge of population-level tolerance and sensitivity to future environmental conditions in the proposed protected areas.</p> <p>Spatial management of a population that is declining may be of reduced value compared with managing other larger or not-reducing populations.</p> <p>Knowledge of plastic capacity across populations could be used to prioritize conservation effort (for example, if a population has enough phenotypic resilience, effort may be better focused in another population).</p>
Promotion of movement, habitat connectivity	<p>Protecting movement corridors, stepping stones and refugia.</p> <p>Increasing landscape permeability to species movement.</p>	<p>Increased connectivity can increase gene flow, the migration of individuals and hybridization, reduce inbreeding and enhance outbreeding.</p>	<p>Yellow-naped Amazons (birds) were investigated at two sites in northern Costa Rica with different degrees of anthropogenic habitat alteration. Both populations displayed the necessary behavioural flexibility in roosting and foraging behaviours to cope with differing concentrations of vegetation. This is a good candidate for enhanced connectivity approaches¹⁰².</p>	<p>Consider the ecological flexibility of the organism in terms of whether enhancing migration corridors will actually yield increased movement and enhance gene flow in the desired direction.</p> <p>If possible, gain an understanding of genetic and phenotypic diversity of disconnected populations before commencing connection, and monitor through time.</p>
Restoration and resilience activities	<p>Activities in which the goal is to restore an ecosystem or to promote resilience (for example an activity to promote the natural maintenance or restoration of the ecosystem) and avoid shifts to alternate stable states.</p>	<p>May result in the addition of new/novel species to a community assembly.</p> <p>May promote increased genetic and phenotypic diversity.</p> <p>May result in reduced genetic and phenotypic diversity if transplants are only sourced from a single (that is, risk of monocultures) or limited number of populations.</p> <p>The success of activities can depend on the composition and balance of trophic levels that are not a part of the activity directly.</p>	<p>Habitat composition can affect the expression of reproductive phenotypes exhibited in desert pupfish. Specifically, habitat structure and availability affect competition and this flows on to influence phenotypic and life-history traits. Management of habitat structure can influence the allocation of spawnings among males in a population and reproductive success¹⁰³.</p>	<p>Restoration actions could account for current phenotypic and genetic diversity. Ideally they should also take into account future fit.</p> <p>Take into account ecosystem attributes that influence plasticity when devising restoration activity.</p> <p>Translocations to regions experiencing rapid environmental change may have enhanced success by choosing individuals on the basis of future phenotypic fit.</p> <p>Climate-adjusted approaches can be implemented to identify and source genotypes that may be ‘pre-adapted’ to future conditions (that is, increase future fit by strategic sourcing on the basis of on climate models).</p>
Managing disturbance regimes	<p>Mitigation of the negative ecosystem impacts of disturbance events.</p> <p>Preventative action to reduce the harmful impacts of disturbance events.</p>	<p>Managing biodiversity requires an understanding of cycles of disturbance, population dynamics and demographics.</p> <p>Biological diversity can potentially be enhanced by disturbance regimes to which ecosystems and their component biota are adapted.</p> <p>High levels of disturbance create environmental stress that may limit biodiversity (for example, via competitive exclusion where a particular species can dominate in a high-stress/low-productivity environment).</p>	<p>The capacity for phenotypic plasticity differs was found to between shrub species following a deforestation disturbance event. <i>Hydrangea aspera</i> exhibited higher leaf plasticity in response to heterogenous environments, compared with <i>Salix etosia</i> and <i>Rubus setchuenensis</i> (ref. 104). This type of knowledge could be used to prioritize conservation effort following disturbance.</p>	<p>Current management timing could shift when considering future phenotypic fit (for example, reproductive phenology of tree species that undergo controlled burning).</p> <p>Sourcing trait variation that is more suitable for future environments may increase future fit. For example, increased fire frequency and intensity predicted under climate change require the introduction of plants from more fire-tolerant populations (that is, resprouters or seeders with shorter time to reproduction).</p> <p>Management of biological disturbances could be enhanced by understanding how the disturbance agent affects phenotypic diversity (for example, tolerance, climatic niche breadth). This would be especially useful in terms of forward thinking with environmental change.</p>

Each management action is described and considered in terms of the ecological and evolutionary processes it may affect. Examples show when plasticity has had an impact on the particular management action, and how consideration of future phenotypic fit could provide a way to incorporate the potential for plasticity (within adaptive capacity) to enhance management outcomes.

informed review of management if actions fail, and further build our knowledge of plasticity. To advance the conversation around planning for plasticity, from the scientific realm to practical reality, we pose the following question:

‘How might existing management practices already be impacted by ecological–evolutionary processes, especially plasticity?’

We already know that management actions have the potential to alter demographic parameters (for example, via assisted recruitment, harvesting) which can, in turn, inadvertently impact future adaptive capacity by altering the distribution of phenotypes and/or genotypes within the population, with implications for natural selection^{69,70}. Being aware of the impacts such actions might have on species and ecosystems enables adjustments in management. As presented in examples (Fig. 3), this can bring important benefits to conservation outcomes when efforts occur against a backdrop of rapid environmental change. The efficacy of existing management strategies might already be impacted by plasticity and could be addressed by considering the above question within the framework of our Solution 3 above. This takes plasticity from a theoretical construct to a practitioner-centred question:

‘How would considering ‘maintenance of phenotypic fit’ influence conservation outcomes?’

This reframing allows actions regularly used in relation to management of ecosystems and species to be considered in terms of their ecological and evolutionary processes. Implementing such a phenotype–environment fit framework illustrates the value in considering how plasticity may enhance outcomes of management actions already occurring or planned (Table 2), rather than suggesting management to enhance adaptive capacity (or adaptive capacity traits) as in previously proposed frameworks³¹.

So how can the consideration of phenotypic fit become an integral part of conservation management protocols? A first step is arming decision-makers with knowledge of how and when plasticity might matter and suggesting a practical way to operationalize plasticity through the lens of an organism’s fit to its environment. This allows practitioners to move from simply considering adaptive capacity, plastic and adaptive processes in management actions to a more forward-looking approach. While beyond the scope of this Perspective, the consideration of phenotypic fit could occur within a broader framework that assesses species vulnerability and the likely need for action (for example, refs. 77,85). These frameworks already possess placeholders for knowledge on plasticity to be incorporated, and in some cases are explicitly included as a component of adaptive capacity (for example, ref. 77). However, using phenotypic fit as an indicator of the potential for plastic and evolutionary processes to keep pace with environmental change allows consideration within broad conservation strategies (both existing and new management actions), as well as allowing prioritization of management efforts. Assessing management priorities would include a biological perspective, as well as economic (for example, potential costs or losses) and social perspectives (for example, cultural importance). These assessments could be used to determine whether an approach that involves planning for plasticity could enhance conservation efforts.

As shown in Fig. 3, not all conservation cases under changing environments will require planning for plasticity. When planning for plasticity may provide benefits, assessment of the attributes indicating fit (Table 1) could be used to explore the current and future fit relative to threats such as climate change, overharvesting and extreme events. Our approach differs from those previously examined under the umbrella of adaptive capacity that use a combination of genetic adaptation and plasticity. Adaptive capacity has classically been about intrinsic ‘ability’

and the use of management actions to enhance adaptive capacity³¹. The framework presented here is ability + environmental change and the impact on fit, with an explicit conversation about the role that plasticity can play in fit.

Conclusions

In this Perspective, we show that planning for plasticity has improved some conservation actions and is not relevant to others. Overall, knowing the potential for plasticity within a population will help to determine whether a given action is likely to succeed, fail or result in unintended consequences. Arming managers with practical knowledge of how and when plasticity might matter is an essential first step. To this end, thinking about plasticity through the lens of an organism’s fit to its environment will be useful. This approach can link widely accepted indicators of extinction risk to prescribed management actions through our proposed filter of the phenotype–environment fit. The formal incorporation of plasticity into management toolkits and a risk–reward/cost–benefit framework represent the ultimate objective, and a road map for putting plasticity into practice starts that journey. This will allow managers to undertake a ‘fit-risk scan’ of planned management actions and flag where caution, or an alternative approach, is needed.

Giving managers the tools to know how plasticity is likely to impact their conservation actions also offers an opportunity to focus the scientific research agenda based on management needs. Future research could target specific knowledge gaps in relation to predicting species or population fit to new environmental conditions. For the scientific community, three research priorities arise from our prescribed approach: (1) undertake targeted fit-for-management research on plasticity and its role in adaptive responses to climate change (see refs. 32,86); (2) identify the abiotic and biotic drivers of plasticity to better predict circumstances under which organisms are likely to show plasticity; and (3) move to field-based research and away from model organisms, which will probably involve the expansion of field trials that incorporate multiple species (for example, climate future plots⁸⁷) or take advantage of spatial variation in environmental change. Collectively, this research effort can provide data to inform managers and decision-makers seeking improved conservation outcomes in the Anthropocene.

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Competing interests

The authors declare no competing interests.

Additional information

Correspondence should be addressed to J. M. Donelson.

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